Analyzing the relationship between the foraging behaviour of two shark species and thermal fronts in the north Atlantic Ocean

Inês Gomes Pereira
Recursos Biológicos Aquáticos
Departamento de Biologia
2017

Orientador
Nuno Miguel Cabral Queiroz, Investigador Pós-Doutoral, CIBIO, FCUP

Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, _____/_____/_____

Agradecimentos

Obrigada **Doutor Nuno Queiroz** por me ter dado a oportunidade de desenvolver este trabalho com o seu grupo, pelos momentos incríveis de descontracção e principalmente pela ajuda nos momentos de maior trabalho.

Obrigada **Mestre Ana Couto** por teres contribuído tanto para este projecto e pela paciência que tiveste comigo.

Ao **Doutor Peter Miller** e restantes pessoas que de alguma forma contribuíram para a realização deste trabalho, o meu muito obrigado.

Obrigada à minha **família**, em especial ao meu **pai** pelo suporte moral e, sobretudo, pelo incentivo à minha formação e realização pessoal.

Obrigada aos meus **amigos** pelos momentos de diversão que me enchiam de força, e foram tantos!

Obrigada **Filipa Borges** por teres um coração tão cheio de bondade.

Obrigada **Natalina**, o teu espírito jovem é uma inspiração para mim.

Diana, tu és a única coisa indispensável à minha vida. O sentimento que nos une não é traduzido em palavras, apenas existe em nós e apenas nós o podemos sentir. Tudo o que eu faço ou deixo de fazer é em função de ti.

À minha **estrelinha polar** que mais do que nunca me fez tanta falta, mais do que nunca foi lembrada e amada. Desculpa por tudo o que ficou por desculpar. Agora que cresci reconheço o valor dos teus actos e o amor que estava por detrás deles. É graças a ti que eu sou quem sou e por isso mesmo eu tento amar-me pelas minhas qualidades e pelos meus defeitos, obrigada. “Um amor que é prioritário nunca pode morrer, só pode crescer”, e o nosso amor cresce assim.

A special thank you for all my **friends from all over the world**! Since I met you, you’ve always kept in touch and gave me support for this great moment of my life. I love you and I’ll never forget you because I brought a peace of each in my heart. People are awaiting us for more solidary actions. Let’s bring more love to this world!

Oumaima, “our souls met before our eyes did”

Este trabalho e todos os anos da minha vida académica são dedicados a vocês.

Henri, my thesis couldn’t start without your amazing version of the Introduction:

“*Sharks are cool, they feed in meats because I taste good. We can study them with negotiation and award them with more meats. The advantages are: we can make them as a cute pet. Marine fronts are awesome, we can visualize them with battleships and nuclear radar. There might be a relation in terms of world domination and the objective of my study is to make sure I can be the next queen Elizabeth*”.

And now it’s my turn…

Resumo

As estratégias de forrageio dos predadores marinhos evoluíram em resposta à distribuição díspar de presas num ambiente vasto, heterogéneo e dinâmico. Essas estratégias permitem que os predadores localizem pontos fortes biológicos, onde a probabilidade de encontrar presas é maior, reduzindo a velocidade e aumentando a taxa de mudança de direcção, de forma a ajustar o esforço de procura em resposta a variações da densidade de presas, o chamado comportamento de procura numa área restrita (PAR), e ao ambiente circundante. Graças às suas características oceanográficas únicas, as frentes oceânicas (gradientes horizontais em propriedades da água, tais como a temperatura, salinidade, entre outras) são ambientes altamente produtivos e consequentemente, pontos fortes de forrageio para muitas espécies marinhas. No entanto, apesar da sua importância como locais de forrageio, o seu valor ecológico para os predadores de topo não é ainda completamente compreendido. Assim, usando mapas frontais compostos de escala fina e dados de rastreio de indivíduos marcados no norte do Atlântico ao longo de 9 anos (2006-2015), pretendemos compreender a influência das alterações dos gradientes térmicos (em frentes oceânicas) no comportamento de forrageio dos tubarões azul (*Prionace glauca*) e anequim (*Isurus oxyrinchus*). Mais especificamente, investigamos a relação entre o FPT dos tubarões como uma medida do esforço de procura dos indivíduos, e parâmetros métricos das frentes (intensidade, proximidade e frequência) utilizando Modelos Aditivos Generalizados Mistos (MAGMs). De acordo com os resultados, valores superiores da intensidade das frentes (F_{comp}) levam a um aumento da intensidade do comportamento PAR (forrageio) dos tubarões azuis. A mesma relação não foi verificada para os anequins provavelmente porque eu apenas analisei quatro indivíduos com um período de rastreio curto. Também se deveria realizar uma análise em escala mais fina para uma melhor compreensão de como os tubarões se relacionam com as frentes termais. Apesar de não se verificar uma relação significativa para os tubarões anequim, podemos considerar as frentes oceânicas como pontos fortes de forrageio preferidos de disponibilidade aumentada de presas. Esta metodologia tem demonstrado ser útil para estudos das relações entre os movimentos e comportamentos dos animais com o meio ambiente.

Palavras-chave: Rastreio de animais, marcação por satélite, temperatura superficial do mar, esforço de busca, gradientes termais, frentes oceânicas, modelo aditivo generalizado misto, *Prionace glauca*, *Isurus oxyrinchus*

Abstract

Foraging strategies of marine predators have evolved to respond to patchy prey distribution in a vast, heterogeneous and dynamic environment. These strategies allow predators to locate biological hotspots, where the probability of prey encounters is higher, reducing travel speed and increasing their turning rates in order to adjust searching effort in response to variations in prey densities, the so-called area-restricted search (ARS) behaviour, and to the surrounding environment. Due to their unique oceanographic characteristics, oceanic fronts (horizontal gradients in water properties, such as temperature, salinity, among others) are highly productive environments and consequently, foraging hotspots for many marine species. However, despite fronts importance as foraging locations, their ecological value for top predators is not yet fully understood. Thus, using fine-scale composite front maps and tracking data from individuals tagged in the north Atlantic over 9 years (2006-2015), I aim to understand the influence of thermal front gradients (in oceanic fronts) on the foraging behaviour of blue (*Prionace glauca*) and mako (*Isurus oxyrinchus*) sharks. Specifically, I investigate the relation between sharks' FPT as measure of individuals' search effort, and front metrics (intensity, proximity and frequency) using Generalized Additive Mixed Models (GAMMs). According to the results, higher frontal intensity (F_{comp}) values lead to an increase in the intensity of ARS (foraging) behaviour in blue sharks. The same relation was not verified for mako sharks, probably because I only analyzed four individuals with a short tracking period. Also a finer-scale analysis should be run in order to better understand how sharks relate to thermal frontal structures. Although no significant relationship was found for mako sharks, we may consider oceanic fronts as preferred foraging hotspots of increased prey availability. This methodology has been shown to be useful for studying links between animal movements and behaviour to the environment.

Key words: animal tracking, satellite-tagging, sea surface temperature, search effort, thermal gradients, oceanic fronts, generalized addictive mixed model, *Prionace glauca*, *Isurus oxyrinchus*

Table of Contents

List of Tables

Table Page

List of Figures

Figure Page

representing the logFPT. The little vertical lines along the *x*-axis indicate the FPT values of individual sharks and the *y*-axis the contribution of the smoother to the fitted values; 35

List of Abbreviations

AVHRR – Advanced very-high-resolution radiometer

ARS – Area-restricted search

Chl-a – Chlorophyll a

corAR1 - AR-1 correlation structure

CSIRO – Commonwealth Scientific and Industrial Research Organization

CTCRW – Continuous-time correlated random walk

F_{comp} – Front composite

FL – Fin length

F_{mean} – Mean frontal gradient

F_{persis} – Front persistence

F_{prox} – Evidence for a feature in proximity

FPT – First-passage time

GAM – Generalized Additive Model

GAMM – Generalized Additive Mixed Model

GLS – Global Locations Sensing

GPS – Global Positioning System

IUCN – International Union for the Conservation of Nature

lmax - Maximum step length

MAR – Mid-Atlantic Ridge

MODIS – Moderate Resolution Imaging Spectroradiometer

PAT / PSAT – Pop-up Satellite Archival tag

P_{front} – Probability of observing a front

PFZ – Polar Front Zone

PPT – Platform transmitter terminal

SeaWiFS – Sea-viewing Wide Field-of view Sensor

SIED – Single-image edge detection

SPOT – Smart Positions Only tag

SST – Sea surface temperature

TDR – Time Depth Recorder

USA – United States of America

UK – United Kingdom

Introduction

Apex predators encompass large pelagic fish species in the top of complex food webs without significant predators except humans. Tunas, swordfish and sharks are examples of apex predators which play a role in structure and stability of marine ecosystem (Myers *et al*., 2007; Stevens *et al*., 2000) through top-down density control of the other species establishing direct and indirect interactions at multiple trophic levels (Heithaus *et al*., 2008; Baum & Worm, 2009). Losing top predators can induce trophic cascades and lead dominance of midlevel consumers, modifying all the previous interactions in the environment. (Pace *et al*., 1999; Worm *et al*., 2003; Frank *et al*., 2005).

Overexploitation of fishing resources has been leading to rapid declines of fish communities as well as shark populations worldwide (Shepherd & Myers, 2005; Dulvy *et al*., 2008; Ferretti *et al*., 2010). The high intensity of long-line and other pelagic fisheries catch many of the same shark species (Bonfil, 1994), which due to their slow growth, late maturity and low reproductive rate have become vulnerable to increased mortality rates (Myers & Worm, 2005).

The knowledge about the ecology of migratory pelagic predators, as the time spent in a given selected area of the sea and its relation with environmental features, allow us to understand their spatiotemporal distribution for the so needed development of conservation and management plans (Block, 2011; Arendt *et al*., 2012; Kessel *et al*., 2014; Afonso & Hazin, 2015). Movement ecology is still giving its first steps (Nathan, 2008) and until several years ago, the information on vertical and horizontal movements, habitat preferences and migrations of large marine species were limited. Nowadays there is an urgent need for this kind of information, especially for pelagic sharks (Sims, 2010; Queiroz, 2012).

Species from this study

The species studied here are in danger mainly because of the high catches rates by fisheries: the blue and shortfin mako sharks. The global blue shark population was evaluated as near threatened by the International Union for the Conservation of Nature (IUCN) Red List, probably due to their high catches by long-line fisheries, mainly as by-catch up to 50% of the total catch weight (Mandelman *et al*., 2008; Mejuto *et al*., 2008). Although they are very abundant and productive than other pelagic sharks (Cortés, 2000;

Frisk, Miller & Fogarty, 2001; Aires-da-Silva & Gallucci, 2007; Anonymous, 2009), there has been a growing concern globally for their conservation.

Because of their high-quality meat and growth in Asian shark fin markets (Dent & Clark, 2015), mako populations had declined since 1986 by commercial and recreational fisheries being the second most heavily caught shark species in the Atlantic Ocean (Cailliet & Bedford, 1983; Hanan *et al*., 1993; Holts *et al*., 1998; Camhi *et al*., 2008) and assessed as Vulnerable by the IUCN Red List.

Still, little is known about the movement ecology of these species. Studies have been limited because of the logistic complications imposed by their oceanic nature, their large-scale horizontal movements, and limits in tracking technology.

Blue shark *Prionace glauca*

Carcharhinidae is one of the biggest families and comprises the one that is considered the most abundant and best-studied shark species, the blue shark (*Prionace glauca* Linnaeus, 1758) (Nakano & Stevens, 2008). This large migratory pelagic shark can be found across the globe in tropic, sub-tropic and temperate zones (Compagno, 1984) and has preference for temperatures from 12 to 20ºC, but can tolerate temperatures from 8 to 29,5ºC (Nakano & Nagasawa, 1996). In the Atlantic Ocean their geographic distribution is extensive, making periodic migrations ranging from Newfoundland to Argentina in the west and from Norway to South Africa in the east (Compagno, 1984) and can be found from the surface to 600 m deep (Campana *et al*., 2011), with the deepest record of 1706 m (Queiroz *et al*., 2017). Their diet is mainly composed by small pelagic fishes and cephalopods, but it can also include invertebrates, bottom fishes, cetaceans, seabirds and small sharks (Compagno,1984; Clarke *et al*., 1996; Stevens, 2000; Henderson *et al*., 2001).

Shortfin mako shark *Isurus oxyrinchus*

The shortfin mako shark (*Isurus oxyrinchus* Rafinesque, 1810) belongs to the family Lamnidae and is found in tropical and temperate seas worldwide (Collette & Klein-MacPhee, 2002; Compagno *et al*., 2005) preferring temperatures from 17 to 22ºC (Compagno, 2001). Like blue sharks, shortfin mako is geographically distributed from Newfoundland to Argentina and from Norway to South Africa in the Atlantic Ocean (Bigelow & Schroeder, 1948; Compagno, 1984) and vertically distributed from the

surface down to at least 500 m depth (Carey *et al*., 1978). As an apex predator, they feed mainly on teleosts (e.g. bluefish, *Pomatomus saltatrix*), but also cephalopods, swordfish, marine mammals, sea turtles and other sharks (Mearns *et al*. 1981; Stillwell & Kohler, 1982; Compagno, 2001; PFMC, 2003).

Telemetry

Ultrasonic telemetry brought the first steps in studying the individual fish behaviour and movements on a small scale (Arnold & Dewar, 2001) with the first publication in 1957 (Trefeden *et al*., 1957). However, it is not possible to obtain details about vertical and horizontal movements and behaviour over longer time periods.

Static array monitoring was considered by Voegeli *et al*. (2001) the best available technique for marine fishes. Lowe *et al*. (2006) used an array of autonomous acoustic receivers to demonstrate whether the tiger sharks (*Galeocerdo cuvier*), Galapagos sharks (*Carcharhinus galapagensis*) and Giant trevally (*Caranx ignobilis*) show affinity to French Frigate Shoals and Midway Atoll from 2000 to 2004. Although the results revealed an effective long-term monitoring of site fidelity and movement patterns of these large marine fishes, some data and also a receiver were lost because of the required maintenance to ensure successful retrieval of data.

Data logging tags were developed in the early 1990s to measure and store large quantities of data and enable vertical and horizontal shark behavioural studies over longer time periods (Sims *et al*., 2010; Wall *et al*., 2007). Studies about shark vertical movements have succeeded. However, the horizontal locations are inaccurate because of the absence of transmitters capable of in-air or underwater position finding (Wilson *et al*., 1992; Bradshaw *et al*., 2007). The biggest limitation of archival tags is the physical recovery by fisheries, mainly because shark recapture is rare and the tag recovering is low (Metcalfe JD & Arnold GP, 1997).

Satellite telemetry has been effective in tracking pelagic air-breathing animals (Mate *et al*., 2000; Nichols *et al*., 2000; Costa *et al*., 2001), and also animals that regularly come to the surface, such as sharks (Eckert & Stewart, 2001; Eckert *et al*., 2002). In the late 1990s, there was the introduction of an electronic tag capable of recording sensor data at a fine temporal resolution over long time periods and with a fishery-independent recovery. Pop-up Satellite Archival tags (PATs or also PSATs) combines an Argos platform transmitter terminal (PTT) to a data-logging sensor. Thus, when detached from

the fish at a pre-programmed date (days/months), it transmits the stored data to the Argos satellite system (Block *et al*., 1998; Lutcavage *et al*., 1999). PAT tags can also record depth, ambient water temperature and solar irradiance for estimating the geographic location (Wildlife Computers[1], 2016). The Argos system uses the Doppler shift calculations of radio transmissions from the tags (Taillade, 1992) providing accurate latitude and longitude (Wilson *et al*., 1992).

For horizontal movement studies, the most effective transmitting tags are Argos-linked tags that transmit near-real-time positions every time the animal is above the water, for multiple years and have positioning error under 1 km (Weng *et al*., 2005). These tags also include a temperature and wet/dry sensor for supporting the transmission of the information about surfacing behaviour and temperature preferences (Wildlife Computers, 2016). These features have advanced studies about a wide range of marine species such as turtles (Hays *et al*., 2006), seals (Stainiland & Robinson, 2008), tunas (De Metrio *et al*., 2005; Stokesbury *et al*., 2007), billfish (Prince & Goodyear, 2006; Hoolihan & Luo, 2007), swordfish (Neilson *et al*., 2009) and sharks (Domeier & Nasby-Lucas, 2008; Campana *et al*., 2009). Such advances in telemetry technology are a key factor in studying animal movement not only in a primarily descriptive way but also quantifying their behaviour and ecological strategies in foraging at different spatial scales.

Area-restricted search (ARS) behaviour

Marine predators are subject to changes in their habitat through different environmental features, such as temperature and light, and their spatial distribution is determined by interactions with other animals, like competitors, predators and prey (Heithaus *et al*., 2002). They are expected to select prey-rich habitats which generally are patchily distributed in space and time (Fauchald, 1999), thus, spending more time within these high prey density areas when compared to other areas where resources are scarce (Fauchald & Tveraa, 2003). For a successful detection of foraging hotspots, there should be an adaptation of the search behaviour by adjusting its pathway in relation to prey temporal and spatial distribution. In other words, marine predators should reduce their travel speeds and increase their turning rates in order to spend more time in the high-density patches. These adaptations are the so-called area-restricted search (ARS) behaviour (Walsh, 1996; Fauchald, 1999; Farnsworth & Beecham, 1999).

[1] Available at www.wildlifecomputers.com

First-passage time (FPT) analysis

Novel analytical methods have been used to study scale-dependent movements in animals (Johnson *et al*., 2002; Fauchald & Tveraa, 2003; Fritz, Saïd & Weimerskirch, 2003; Nams, 2005; Tremblay *et al*., 2007; Breed *et al*., 2009) identifying if they are foraging, mating or resting through the tortuosity of the path. A useful indicator of ARS behaviour is the First-passage time (FPT) (Fauchald & Tveraa, 2003) that is, by definition, the time an animal requires to cross a circle of a given radius along its trajectory (Johnson *et al*., 1992). This circle is moved along the path of the animal at equidistant points, repeatedly with increasing radius. More area of the trajectory is covered by the increasing circle resulting in higher FPT values. The radius that best differentiates between low FPT areas and high FPT areas (transitory areas from intensive search areas) is chosen. It is also expected a higher FPT value in areas with increased sinuosity and/or decreases in movement speed than in areas with faster and more straight-line movements. FPT analysis has been applied in studies to identify ARS behaviour in marine mammals and mostly in seabirds (Thums, Bradshaw & Hindell, 2011; Dragon *et al*., 2012). Pinaud *et al*. (2008) showed that FPT analysis can be efficiently used with Argos and GPS as a method for studying animal movement, detecting when the animal changes speed and sinuosity when in contact with a high density of resource, or when the animal reacts to the patch boundary (Benhamou, 1992).

Habitat preference and marine fronts

Environmental factors are often associated with fish diversity and abundance. An interaction between these factors can result in a very important phenomenon known as oceanic fronts. A frontal structure is formed by the meeting of two different water masses creating a convergence at the surface or bottom boundary, which generates a sharp change in the physical parameters, for example temperature and salinity (Largier, 1993), marking physical and chemical boundaries that correspond to biogeographical transition zones (Mann & Lazier, 1991). Such features increase the turbulence, mixing both laterally and vertically, resulting in the input of nutrients which in combination with warm waters (21–24ºC) and sufficient oxygen concentrations (>2 ml l^{-1}), enhance biological productivity (Oschlies & Garçon, 1988; Franks, 1992; Yoder *et al*., 1994; Acha *et al*. 2004; Worm *et al*., 2005). These conditions determine prey distribution and consequently allocate a high diversity of open-ocean top predators to oceanic fronts (Worm *et al*. 2003, 2005; Vlietstra, 2005; Boyce *et al*., 2008) where they find favorable feeding conditions. Some studies found it in seabirds (Guinet *et al*., 1997; Hamer *et al*., 2009, De Monte,

2012), marine mammals (Bost *et al*., 2009; Field *et al.,* 2001; Scales, 2014b), turtles (Chambault *et al*., 2015) and fishes like tunas (Fiedler & Bernard, 1987; Royer *et al*., 2004), swordfish (Podesta *et al*., 1993) and sharks (Sims & Quayle, 1998; Etnoyer *et al*., 2004; Priede & Miller, 2009).

Marine fronts are known attraction areas for sharks in all oceans. For example, porbeagle sharks (*Lamna nasus*) aggregate along marine fronts of the northwest Atlantic during spring (Campana and Joyce, 2004); salmon sharks (*Lamna ditropis*) revealed more ARS behaviour when migrating in the highly productive Subarctic Alaska Gyre than those that migrated to the low productive Subtropical Gyre (Weng *et al*., 2008); whale shark occurrence was significantly influenced by sea surface temperature (SST) and strong thermal gradients, indicating that whale sharks spent more time in frontal regions associated with upwelling systems in the Gulf of California, Mexico (Ramírez-Macías *et al.*, 2017).

The Atlantic current system, among many other factors, is known to influence the distribution of blue sharks (Stevens, 1990; Kohler & Turner, 2008). Queiroz *et al*. (2012) tracked blue sharks in the northeast Atlantic in order to determine their vertical niche and horizontal movements and if it is influenced by oceanographic features. Sharks were tagged with PAT tags between July 2006 and June 2008 in the English Channel off south-west England and off southern Portugal. In general, all sharks moved south-west from the tagging sites, with only one shark remaining in the continental shelf dominated by the presence of tidal fronts. It was evident a site fidelity to localized high-productive regions where fronts were present, for example, one shark displayed an initial southward movement towards the African coast and continued to move south reaching the Western Sahara upwelling system in mid-July 2008. Blue sharks spent more time near the surface during the day and night, but displayed a distinct normal diel component in maximum depth, repeatedly displayed during the day below the thermocline (~100m), most probably for feeding, while diving above the thermocline during night hours.

A study was carried about shortfin mako shark in the western north Atlantic Ocean off the coast of the northeastern United States of America (USA) and the Gulf of Mexico for a detailed investigation on vertical movements included in the context of horizontal movements (Vaudo *et al*., 2016). Eight sharks were tagged between 2004 and 2012 with PAT tags. Vertical movements were strongly associated with ocean temperature, with a narrow distribution of shallow depth in cooler bodies of water and a greater range of depths in the warmer ones. Two sharks were tracked for several months in the western

north Atlantic and moved southerly, leaving the region of the continental shelf during the autumn and showing seasonal horizontal movements from cooler to warmer waters. The other three sharks tagged in this region remained over the continental shelf. The two sharks tagged in the mouth of the Gulf of Mexico traveled northeast into the deeper waters between Campeche Bank and West Florida Shelf. Then, they took different directions with one shark moving to the northern Gulf of Mexico and the other shark moving to the southwestern Gulf of Mexico. In similarity, Block *et al.* (2011) reported the same movement, from cooler water to warmer water, in the eastern north Pacific Ocean associated with seasonal changes in water temperature and productivity, and in the southeastern Indian Ocean where Rogers *et al*. (2015) observed northward movements.

Thermal fronts visualization

The analysis of oceanographic features has been based on some important environmental predictors as SST and chlorophyll a (chl-a) that play a significant role in species richness patterns due to optimal thermal ranges and food availability (Etnoyer *et al*., 2004; Worm *et al*., 2005; Mitchell *et al*., 2014). However, there is some concern about the capacity of these traditional measurements for predicting distributions of marine predators (Burger, 2003; Grémillet, 2008) because visible and infrared satellite data are severely affected by cloud cover. Recently, the composite front mapping (Miller, 2009; Miller & Christodoulou, 2014; Scales *et al*., 2015) was developed to identify discrete oceanographic frontal features by combining the locations of frontal fragments derived from all clear sea patches in a sequence of satellite images with full resolution of dynamic features that are not blurred. Simplifying this, composite front maps result from the combination of all fronts detected on a sequence of images from few days into a single map, with the information about location, strength and persistence. Full methodology can be found in Miller (2009).

An example of how this approach can be effective on the characterization of frontal activity is the study carried by Miller *et al*. (2015). In this study, seven basking sharks were tracked with PAT tags off north-west Scotland and south-west England between May and August in 2001 and 2002, in combination with high-resolution composite front mapping (1 km pixel size; 7-day composites; Miller, 2009) to investigate levels of association with fronts occurring over two spatiotemporal scales (broad-scale, seasonally persistent frontal zones and contemporaneous thermal and chl-a fronts). The tracked sharks were more likely to be found in association with seasonally persistent

frontal zones and their habitat selection was more influenced by contemporaneous mesoscale thermal and chl-a fronts. Seasonal front frequency metrics were significant predictors of shark presence, both over seasonal timescales and in near real-time, in frontal activity and indicated that sharks may return to spatiotemporally predictable foraging grounds where they foraged previously.

Objectives

Despite fronts' importance as foraging locations, their ecological value for top predators is not yet fully understood, mainly because the majority of them has low population abundance, which makes difficult to get sufficient data to support studies aiming to understand the relation between movements and behaviour with the environment (Pade *et al*., 2009). Thus, using fine-scale composite front maps and tracking data from individuals tagged in the north Atlantic over 9 years (2006-2015), I aim to understand the influence of frontal activity on blue and mako sharks' foraging behaviour. Specifically, I will investigate the relation between sharks' FPT as a measure of individuals' search effort, and front metrics (intensity, proximity and frequency) using Generalized Additive Mixed Models (GAMMs). This study will provide novel information on the spatial and temporal distribution of two top predators, providing the basis for the development and establishment of adequate management and conservation strategies.

Materials and Methods

Shark tagging

I used tracking data from 48 individuals from two different shark species, the blue (*Prionace glauca*) and shortfin mako (*Isurus oxyrinchus)*. Capture and tagging methodology are fully described in Queiroz *et al*. (2016) and Vandeperre *et al.* (2014). Sharks were tagged in three different regions, in the north-eastern Atlantic (off southern England and mainland Portugal), north-western Atlantic and mid-Atlantic in the Azores archipelago.

A total of 12 blue (S1 to S12) and 2 mako (M1 and M2) sharks were tagged between 2006 and 2011 with SPOT tags (SPOT5, Wildlife Computers, Redmond, WA, USA) attached to the first dorsal fin with stainless steel bolts, neoprene and steel washers, and steel screw-lock nuts. A total of 11 blue (S13 to S23) and 2 mako (M3 and M4) sharks were tagged with KiwiSat 202 PPTs (Sirtrack, New Zealand) between 2014 and 2015 following the same methodology.

The remaining 21 blue sharks (A1 to A21) were tagged off an auxiliary 7 m, low gunnel, fiberglass boat, at the surface after immobilization and induction of tonic immobility (Meyer et al., 2010), between 2009 and 2012 in the Azores archipelago. SPOT tags were attached to the dorsal fin of sharks measuring 127 to 211 cm Fork Length (FL) through four nylon threaded rods fixed through stainless steel nuts. Three females (A4, A5 and A6) were double tagged with SPOT and PAT tags (MK10-PAT, Wildlife Computers, Redmond, WA, USA) measuring 142 to 175 cm FL. All tags were pre-programmed to detach from the shark after a period of days.

Track reconstruction

Track reconstruction of both blue and mako sharks are described in detail in Queiroz (2016). Geographical positions of SPOT and KiwiSat 202 tags' transmissions were obtained through the Argos system. Argos calculates locations by measuring the Doppler Effect on transmission frequency and provides different LCs (LC 3, 2, 1, 0, A, B and Z) based on error calculation (Argos User's Manual[2]). The tracks were interpolated in order to obtain daily positions. The LC data were analyzed point-to-point with a 3 $m \cdot s^{-1}$ speed filter. The raw Argos locations were processed with a Continuous-time correlated random walk (CTCRW) state-space model producing the animal daily positions. CTCRW state-

[2] Available at www.argos-system.org/manual

space model couples a mechanistic model of movement to the data and inferences of the animal positions can be made. Locations are based on the probability of presence at a certain point given its current state (Patterson *et al*., 2008). These Argos positions were parameterized with the K error model parameters for longitude and latitude using “crawl” package in R (R Core Team, 2016). Figure 1 and 2 show the spatial distributions of blue and mako sharks, respectively.

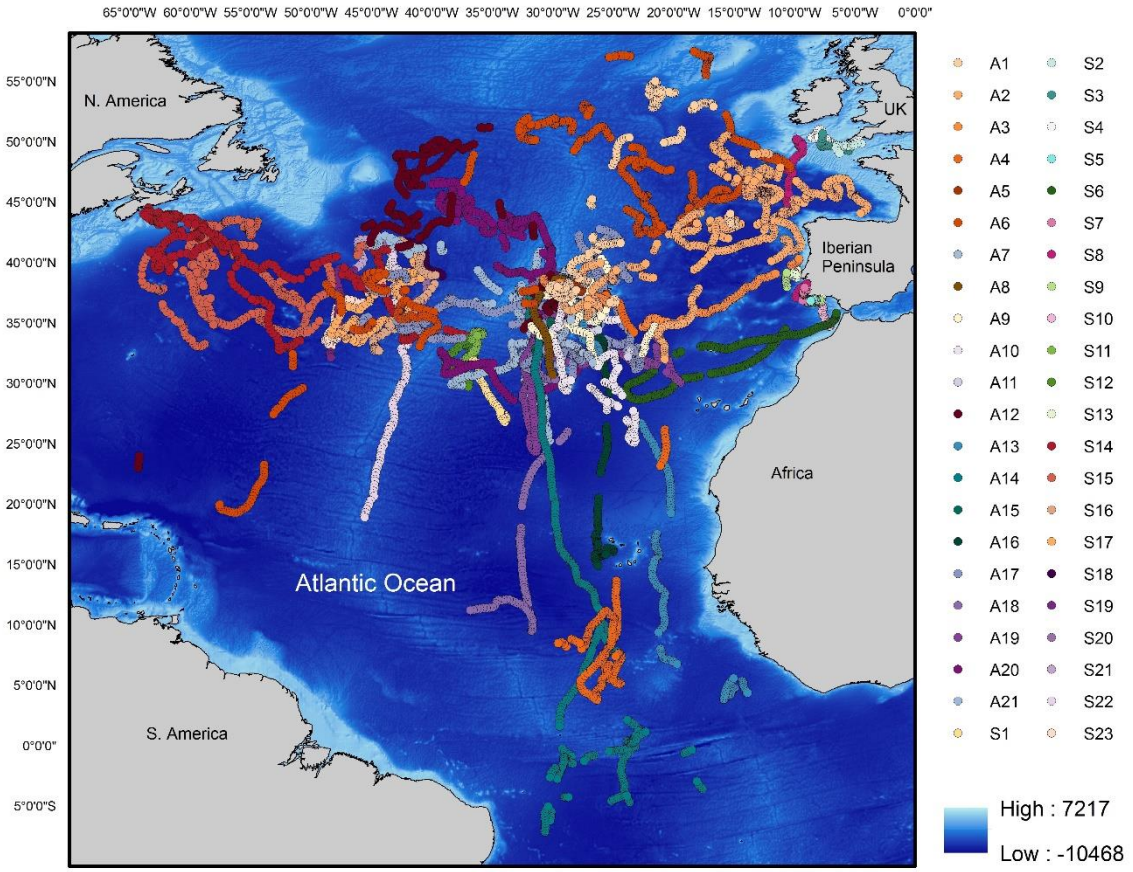


Fig. 1 – Spatial distributions of satellite-tracked blue sharks *Prionace glauca* (S1 to S23 and A1 to A21) between 2006 and 2015 in the north Atlantic Ocean.

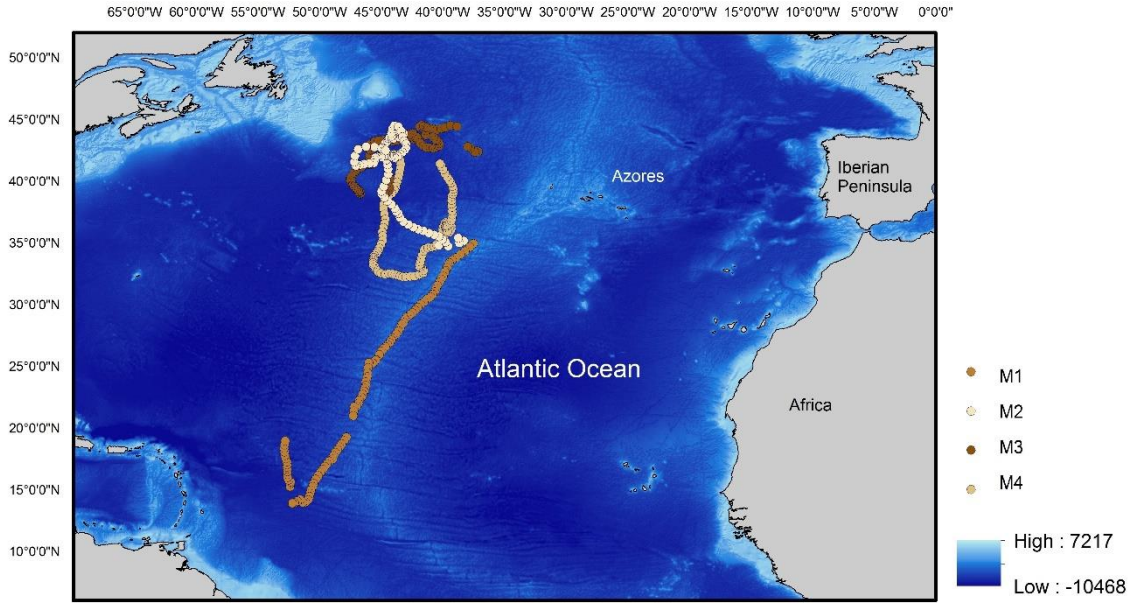


Fig. 2 - Spatial distributions of satellite-tracked mako sharks *Isurus oxyrinchus* (M1 to M4) between 2011 and 2014 in the north Atlantic Ocean.

FPT analysis

The FPT analysis were performed using the *fpt* function of the "adehabitatLT" package in R v.0.99.892 (Fauchald & Tveraa, 2003; R Core Team, 2016) for sharks' search effort quantifications. We split the track in sections to find the maximum step length (lmax) of each part and set the maximum of distance traveled between sections as the maximum radius *r*. After this, FPT values were calculated by moving the circle at variable distance for spatial scales *r* from 25 km (0.04 km to 2*lmax) at increments of 0.10*lmax (Bradshaw *et al*., 2007). FPT is found by measuring the time lag between the first crossing of the circle backward and forward along the path (removing the first and final points of the track where the FPT is unknown) with higher values for more intensively searched areas. FPT is a scale-dependent measure of sharks' search effort, so that the ARS scales were determined by the value of *r* with the maximum variance in the log-transformed FPT values to ensure the variance is independent of the magnitude of the mean FPT (var[log (FPT)]). Thus, for each individual track, I plotted the logFPT against *r* and identified peaks in variance. By the analysis, I was able to locate where sharks showed more intense foraging behaviour during their tracking period (Fauchald & Tveraa, 2003).

Composite front mapping

In order to create a composite front map, some parameters need to be calculated. Single-image edge detection (SIED) algorithm (Cayula & Cornillon,1992) is used for processing SST scenes within 7-day window from Advanced very-high-resolution radiometer (AVHRR) and Sea-viewing Wide Field-of-view Sensor (SeaWiFS) data with a temperature difference threshold of at least 0.4°C (conversion of raw satellite data into calibrated ocean temperature and colour products is summarized in Appendix A in Miller, 2009). The composite duration appears to be long enough to provide the multiple observation of the most genuine features, and not too long that features are obscured by multiple adjacent observations (Miller, 2009). An example of a composite front map can be seen in figure 3. The short-period composites were used in this study because I aim to examine dynamic features instead of static features, which were examined in past studies using composites of weeks or months (e.g. Ullman & Cornillon, 1999), and also because long-period composites can mask neighboring features (Miller, 2009).

The processed SST are then composited to calculate the mean frontal gradient map F_{mean} derived from the sequence of front maps, the probability of observing a front at a particular pixel during the sequence P_{front} and the evidence for a feature in proximity F_{prox}. With this information, the front persistence $F_{persist}$, that is defined both by the gradient and the frequency a front is observed at the same location, can be calculated. On a final stage, the front composite F_{comp} map is generated by combining all the previously referred parameters and provide a better visualization of the oceanic features (Miller, 2009, 2016). Figure 3 show an example of a composite front map.

Using fine-scale SST composite front maps I obtained information on front metrics for each shark tracking period by calculating the mean F_{comp} using *Cell statistics* from the Local toolset in ArcGIS, which calculates the mean per-cell from multiple rasters, in other words, it gives the mean raster calculated from the rasters correspondent to a shark tracking period. The raster value for each point of the tracks was also calculated using *Extract value to points* from the Extract toolset in ArcGIS, which extracts the cell values of a raster based on a set of point features. Raster values were recorded in the attribute table of an output feature class and used in further analysis.

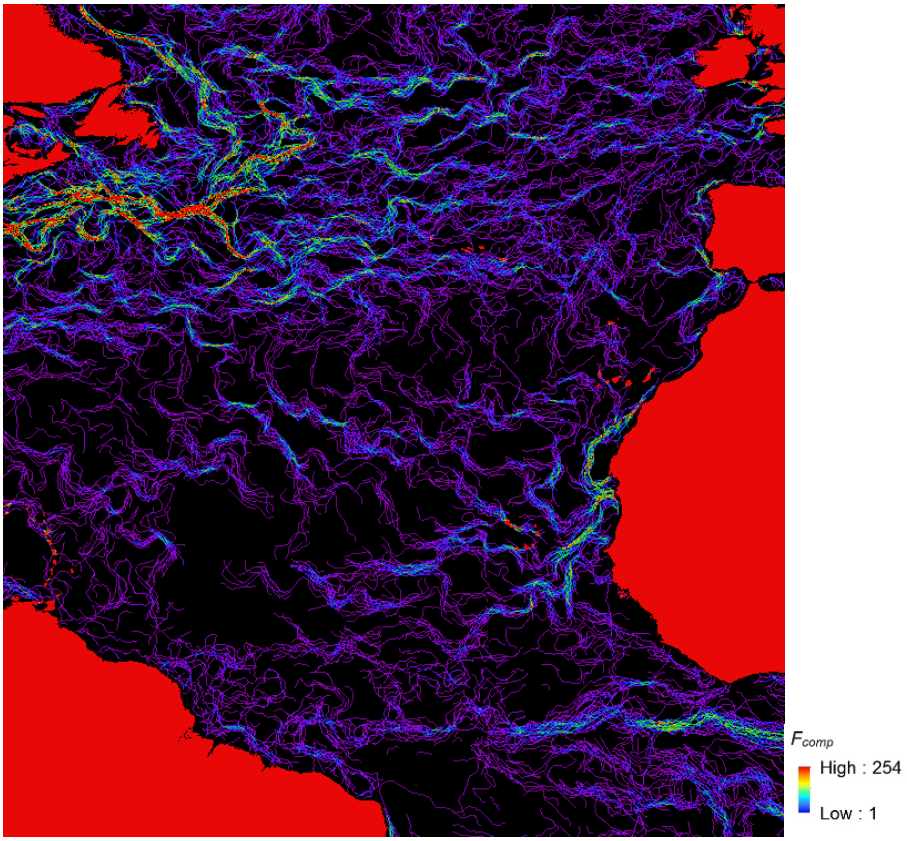


Fig. 3 – Example of a composite front map with a 7-day window showing thermal fronts in the north Atlantic Ocean (26 June 2010 to 2 July 2010).

GAMM design

To analyze the spatial relationship between F_{comp} and FPT, a GAMM was applied separately for each of the species using the "mgcv" package in R (Wood, 2006; Zuur *et al.,* 2009; R Core Team, 2016).

GAMMs are an extension of Generalized Additive Models (GAMs) (Hastie & Tibshirani, 1990) incorporating a smooth interaction of space and time with some of the predictors being treated as random factors. They allow for nonlinear responses in the data and their use have been proposed for studies where there are differences in measured parameters for different individuals (Stroud *et al.,* 2001; Gelfand *et al.,* 2005; Strickland *et al.,* 2011).

In each model, individual sharks (ID) was treated as a random factor while the log-transformed F_{comp} and FPT were set as fixed effect variables. Instead of treating the data as a single individual I want the model to treat each individual shark as a unique time series, that is why I use shark (ID) as a random factor. The logFPT was set as the response (or dependent) variable while logF_{comp} was set as the explanatory (or independent) variable. Variable logF_{comp} was modeled using a smoothing function

estimated by thin-plate regression spline. The optimal amount of smoothing was automatically estimated using cross-validation (Wood, 2006). An auto-regressive process of order 1 (corAR1) was added to allow the temporal autocorrelation in the dataset. For example, it assumes that a track position at time t is dependent on the magnitude of the position at time t-1 (Zuur *et al*., 2009). Our final formula was:

$$\text{logFPT} \sim s(\log F_{comp})$$

The 95% Bayesian confidence intervals were estimated following Wood (2006). Model validation and all the previously mentioned steps were performed following Zuur *et al*. (2009) in R (Core Team, 2016).

Results

The 48 individuals resulted in 8429 d of tracking data and an average trip duration of 175,60 d. In general, blue and mako sharks displayed a broad distribution among the different north Atlantic regions. The majority of the individuals were oceanic, with exception of sharks S2-S4 that remained in the south-west England, and sharks S5, S7, S9, S10 and S13 that did not leave the southern Portugal area. The longest deployment registered was from a female (A6) that traveled an estimated 28139 km over a 952 d tracking period and the shortest deployment was from the female S5 that only traveled 113 km during 23 d. Blue sharks tagged in Azores displayed extensive movements, with the female A14 traveling straight to the south and reaching the southern hemisphere. Eight individuals (four females and four males) were tracked for over a year (A1, A2, A6, A12, A14, A17, A20 and A21) allowing the observation of a full season cycle. Only the mako M1 moved southeast and had the longest tracking period among mako sharks. Distribution patterns tended to be more northwest in summer while it was more south-easterly in winter for both species. Table 1 summarizes the information about all the individuals used in this study.

Table 1 – Summary data from the 48 individual sharks tagged between 2006 and 2015 in the north Atlantic Ocean.

Name	Species	Size (cm FL)	Sex	Location tagged	Tag	Tagging date	Days-at-liberty	Distance (km)
M1	*Isurus oxyrinchus*	210	F	Oceanic	SPOT 5	5 Sep 2011	58	3773
M2	*Isurus oxyrinchus*	200	M	Oceanic	SPOT 5	8 Sep 2011	50	3849
M3	*Isurus oxyrinchus*	185	F	Oceanic	KiwiSat 202	13 Aug 2015	32	3372
M4	*Isurus oxyrinchus*	180	M	Oceanic	KiwiSat 202	9 Jun 2014	23	3455
S1	*Prionace glauca*	210	F	Oceanic	SPOT 5	29 Aug 2011	46	750
S2	*Prionace glauca*	186	F	England	SPOT 5	15 Aug 2006	8	231
S3	*Prionace glauca*	170	F	England	SPOT 5	18 Aug 2006	14	302
S4	*Prionace glauca*	160	F	England	SPOT 5	31 Aug 2006	21	525
S5	*Prionace glauca*	145	F	Portugal	SPOT 5	1 Jun 2009	23	113

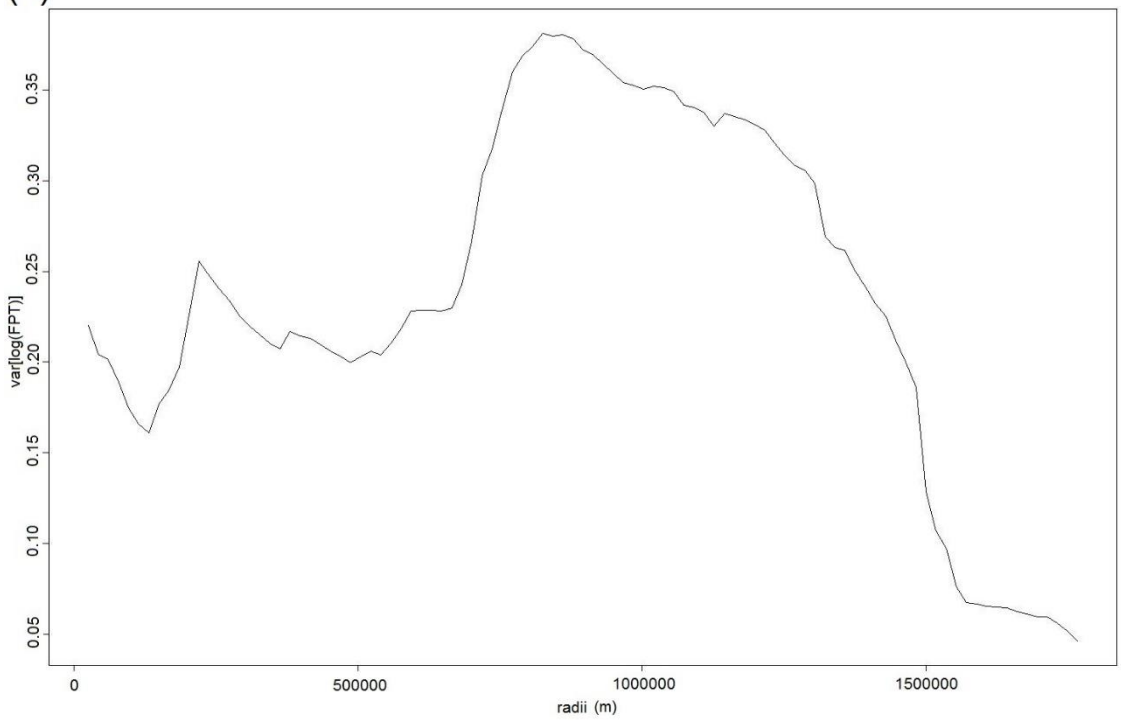
S6	*Prionace glauca*	220	M	Portugal	SPOT 5	2 Jun 2009	102	3379
S7	*Prionace glauca*	90	M	Portugal	SPOT 5	10 Oct 2006	23	173
S8	*Prionace glauca*	130	F	Portugal	SPOT 5	6 Jun 2008	101	157
S9	*Prionace glauca*	130	M	Portugal	SPOT 5	17 Jun 2008	112	835
S10	*Prionace glauca*	125	F	Portugal	SPOT 5	26 May 2009	12	254
S11	*Prionace glauca*	190	F	Oceanic	SPOT 5	30 Aug 2011	18	510
S12	*Prionace glauca*	220	F	Oceanic	SPOT 5	2 Sep 2011	33	969
S13	*Prionace glauca*	120	F	Portugal	KiwiSat 202	20 May 2015	39	558
S14	*Prionace glauca*	205	M	Oceanic	KiwiSat 202	9 Jun 2014	213	8968
S15	*Prionace glauca*	145	F	Oceanic	KiwiSat 202	12 Jun 2014	225	10070
S16	*Prionace glauca*	220	F	Oceanic	KiwiSat 202	5 Jun 2014	407	1487
S17	*Prionace glauca*	220	F	Oceanic	KiwiSat 202	5 Jun 2014	93	3394
S18	*Prionace glauca*	230	F	Oceanic	KiwiSat 202	5 Jun 2014	10	525
S19	*Prionace glauca*	215	F	Oceanic	KiwiSat 202	14 Jun 2014	20	655
S20	*Prionace glauca*	210	F	Oceanic	KiwiSat 202	7 Jun 2014	15	767
S21	*Prionace glauca*	190	F	Oceanic	KiwiSat 202	7 Jun 2014	10	479
S22	*Prionace glauca*	220	F	Oceanic	KiwiSat 202	9 Jun 2014	56	769
S23	*Prionace glauca*	220	F	Oceanic	KiwiSat 202	11 Jun 2014	42	1560
A1	*Prionace glauca*	127	F	Azores	SPOT	19 Feb 2009	877	14494
A2	*Prionace glauca*	139	F	Azores	SPOT	19 Feb 2010	616	16907

A3	*Prionace glauca*	148	F	Azores	SPOT	26 Feb 2009	90	2637
A4	*Prionace glauca*	175	F	Azores	Double	26 Aug 2010	226	8275
A5	*Prionace glauca*	142	F	Azores	Double	26 Aug 2010	30	911
A6	*Prionace glauca*	145	F	Azores	Double	26 Aug 2010	952	28139
A7	*Prionace glauca*	130	M	Azores	SPOT	2 Dec 2009	42	973
A8	*Prionace glauca*	168	F	Azores	SPOT	16 Oct 2009	36	1213
A9	*Prionace glauca*	133	M	Azores	SPOT	16 Oct 2009	206	5041
A10	*Prionace glauca*	201	M	Azores	SPOT	16 Oct 2009	161	5108
A11	*Prionace glauca*	156	M	Azores	SPOT	2 Dec 2009	82	2245
A12	*Prionace glauca*	178	F	Azores	SPOT	20 Aug 2010	579	15498
A13	*Prionace glauca*	164	M	Azores	SPOT	20 Aug 2010	244	6892
A14	*Prionace glauca*	180	M	Azores	SPOT	20 Aug 2010	381	13066
A15	*Prionace glauca*	140	M	Azores	SPOT	20 Aug 2010	126	2364
A16	*Prionace glauca*	183	M	Azores	SPOT	20 Aug 2010	116	3846
A17	*Prionace glauca*	183	M	Azores	SPOT	20 Aug 2010	524	15066
A18	*Prionace glauca*	159	M	Azores	SPOT	20 Aug 2010	212	5994
A19	*Prionace glauca*	207	M	Azores	SPOT	20 Aug 2010	228	6710
A20	*Prionace glauca*	172	M	Azores	SPOT	20 Aug 2010	369	12451
A21	*Prionace glauca*	211	M	Azores	SPOT	20 Aug 2010	526	14500

FPT analysis

I performed FPT analysis to quantify sharks' search effort. Peaks in varFPT/area were observed for all the individuals (Table 2, Annexes), with maximum variance values ranging from 0.04 to 2.49 and FPT radius between 25.00 and 824.70 km. For mako sharks, the FPT radius ranged from 58.00 to 268.55 km, while for blue sharks (S1-S23) the FPT radius ranged from 25.00 to 604.64 km. Blue sharks tagged in the Azores (A1-A21) had the greatest range with FPT radius from 25.00 to 824.70 km. In Figure 4 we can see an example of the resultant plots for shark A14 after running the FPT analysis.

(a)



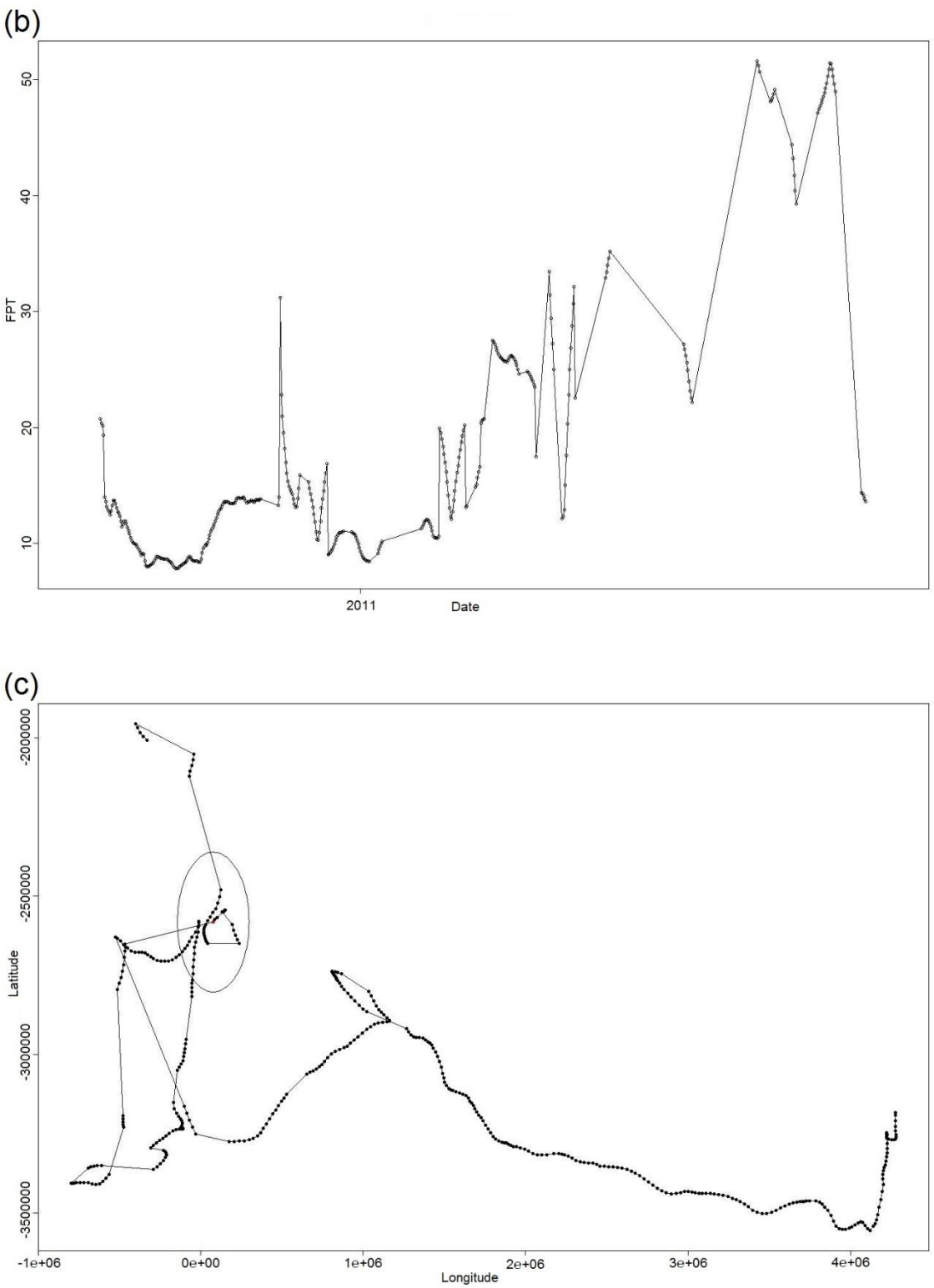


Fig. 4 – Example track of shark A14 with (a) the variance in first-passage time for circles of different radius peaking at 824,70 km; (b) first-passage time for each move across an 824,70 km radius circle; and (c) recorded shark positions with the circle of 824,70 km radius.

Composite front maps

In order to understand how the gradients of SST in the north Atlantic relates to individual shark distribution patterns, composite front maps were generated for each individual for their entire tracking period. Associations of individual sharks with the respective composite front map showed a preference for highly productive areas such as the Gulf Stream, North Atlantic Current, Azores islands, Mid-Atlantic Ridge (MAR) southwest of the Azores and the Iberian Peninsula. This site fidelity is evident for some individuals, for example, shark S14 tagged in the Mid-Atlantic moved to the Gulf Stream in the beginning of August until mid-November (Figure 5).

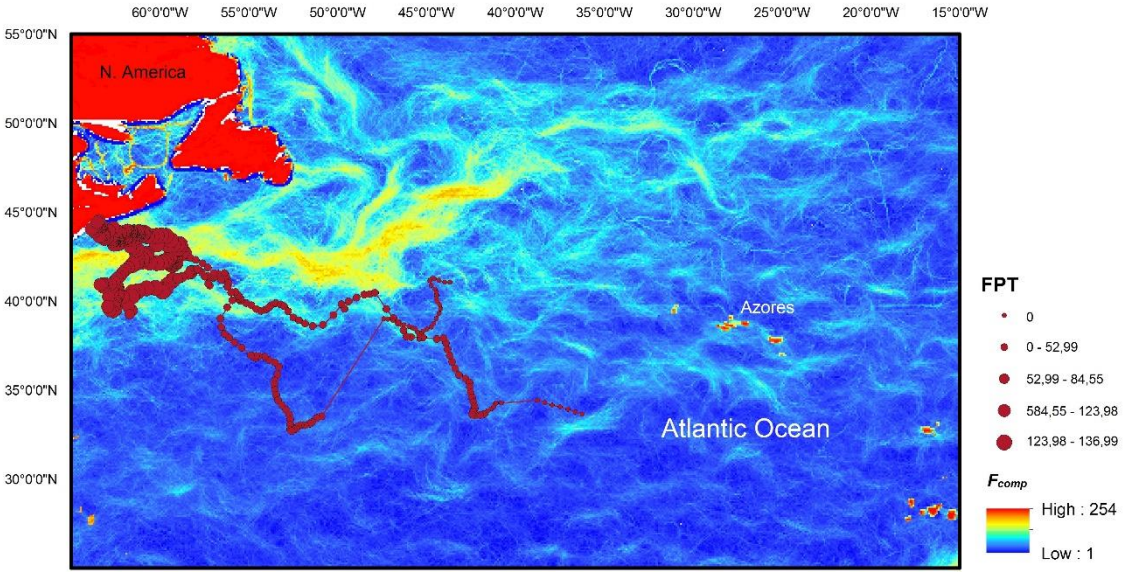


Fig. 5 – Geographical locations with FPT and correspondent F_{comp} of shark S14 (9 June 2014 to 8 January 2015).

Shark A12 tagged in Azores spent the winter in this region and then moved northward exploring the Gulf Stream in east and south of the Flemish cap during summer. About seven months after being released, shark A12 returned to the tagging region in the Azores where it spent the autumn and winter, moving northward in February and after a 220 d gap period, A12 appeared near eastern central America (Figure 6).

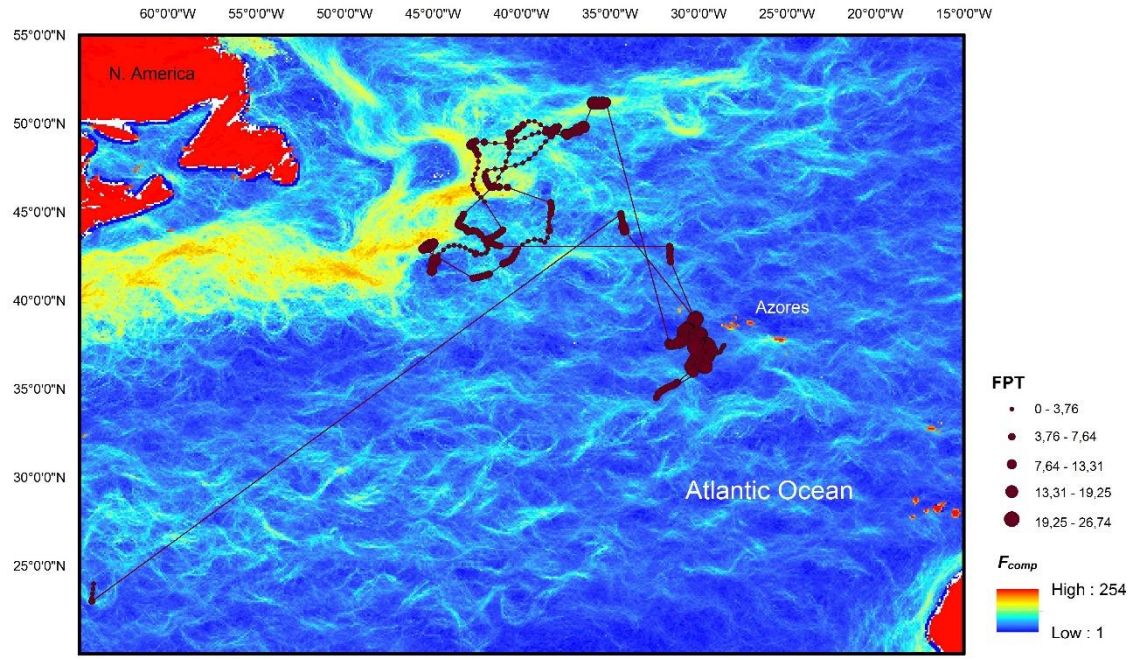


Fig. 6 – Geographical locations with FPT and correspondent F_{comp} of shark A12 (9 December 2009 to 23 June 2011).

Shark M2 moved northwest from the tagging location to the Gulf Stream in the early autumn until the end of the tracking period (Figure 7).

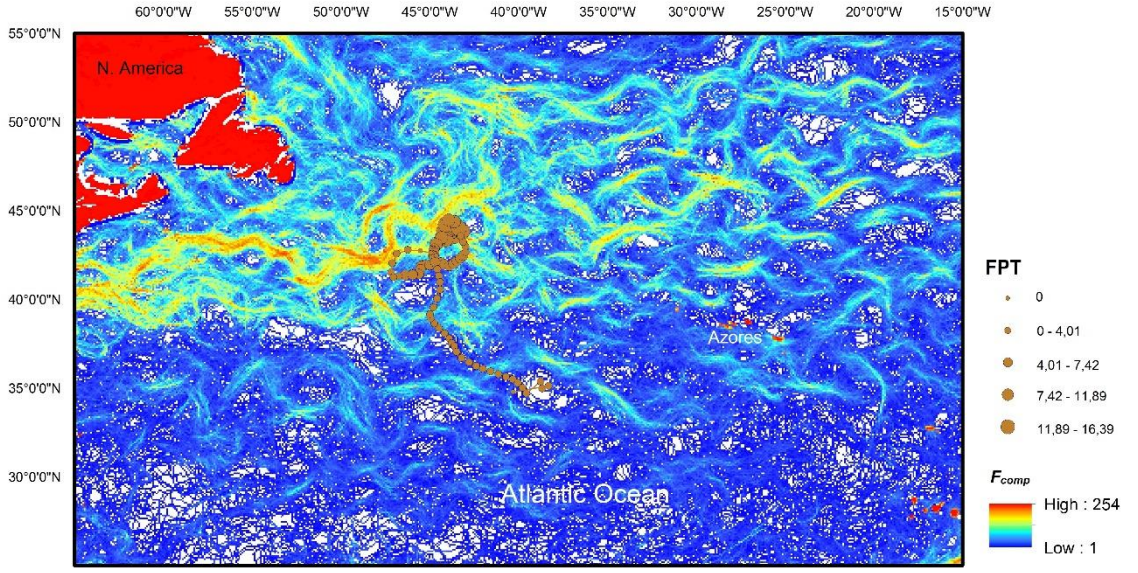


Fig. 7 – Geographical locations with FPT and correspondent F_{comp} of mako M2 (10 September to 28 October 2011).

Relation between search effort and thermal fronts

Finally, for a better understand of the influence that thermal fronts have in the foraging behaviour I performed a GAMM for each of the studied species. GAMM results are summarized in Tables 3 and 4.

Table 3 – Summary of model results for blue sharks. Estimated parameters from the final generalized additive mixed model and numerical output for the smoothing function. edf: estimated degrees of freedom; Scale est: estimate scale parameter; R^2: explanation for deviance; Scale est: variance of Residuals.

Parametric coefficients:				
	Estimate	**Std. Error**	***t* value**	**Pr(>|t|)**
(Intercept)	1.49	0.07	22.29	<2e-16
Approximate significance of smooth terms:				
	edf	**Ref.df**	***F***	**p-value**
s(logF_{comp})	5.02	5.02	17.83	<2e-16
R^2(adj) = 0,22		Scale est. = 0.08	n = 971	

Table 4 – Summary of model results for mako sharks. Estimated parameters from the final generalized additive mixed model and numerical output for the smoothing function. edf: estimated degrees of freedom; Scale est: estimate scale parameter; R^2: explanation for deviance; Scale est: variance of Residuals.

Parametric coefficients:				
	Estimate	**Std. Error**	***t* value**	**Pr(>|t|)**
(Intercept)	1.70	0.09	19.12	<2e-16
Approximate significance of smooth terms:				
	edf	**Ref.df**	***F***	**p-value**
s(logF_{comp})	2.86	2.86	2.06	0.11
R^2(adj) = -0.01		Scale est. = 0.10	n = 265	

According to the GAMM results for blue sharks, higher frontal intensity (F_{comp}) values lead to an increase in the intensity of ARS (foraging) behaviour. The R^2 value for the

model was 0.22, indicating that about 22% of the variation in logFPT can be explained by the logF_{comp}. The variance of the residuals is 0.08. The smoother s(logF_{comp}) was found to be statistically significant at the 5% level (F=17.83, p<2e^{-16}) and thus contributed to model sharks' logFPT (Figure 8). The optimal number of degrees of freedom for the smoother was 5.02, confirming the non-linear relationship between FPT and F_{comp}.

There was a clear effect of frontal intensity on ARS (foraging) behaviour (Figure 8). The smoother starts with the minimum value of ~0.50, kept stable and showed a sharp increase at ~1.60 until it reaches a peak at ~2.25.

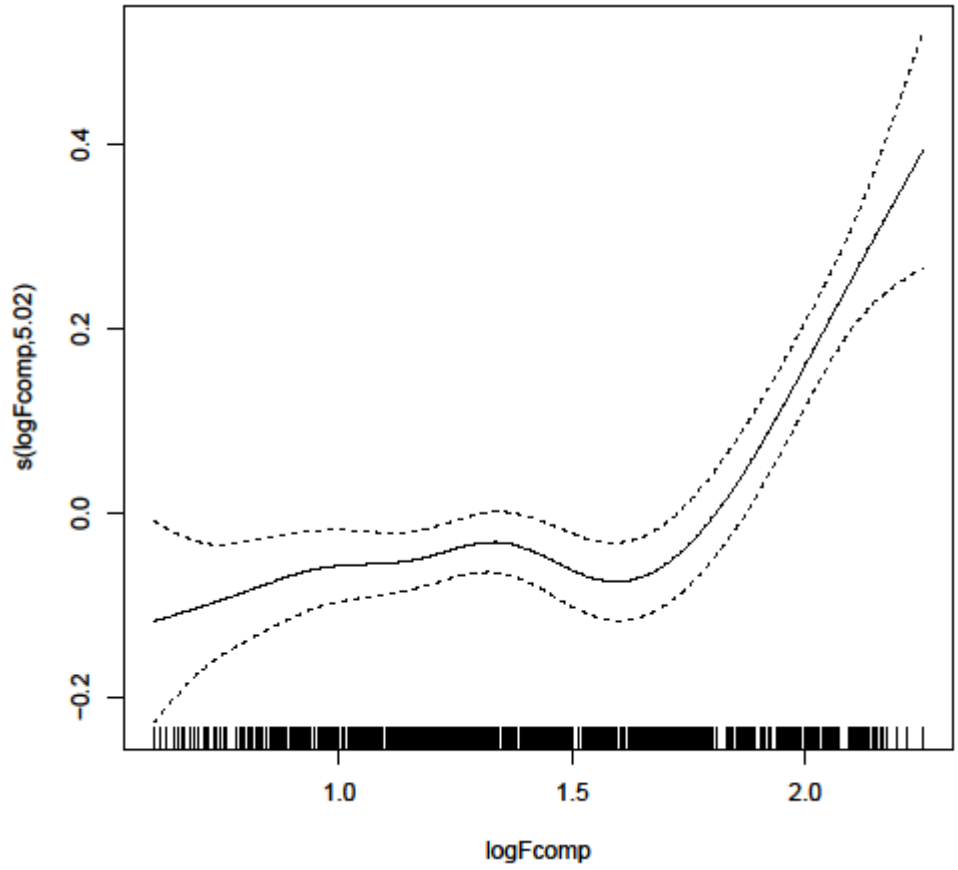


Fig. 8 – Modelling the relation between F_{comp} and FPT with a Generalized Addictive Mixed Model (GAMM) for blue sharks. F_{comp} had a smoothing term significantly different from zero (p<0.001) and thus contributed to model sharks' FPT. An initial stable relation between FPT and F_{comp} was observed, followed by a sharp increase in FPT with the increase of F_{comp}. Dashed lines represent 95% confidence intervals above and below the solid line representing the logFPT. The little vertical lines along the *x*-axis indicate the FPT values of individual sharks and the *y*-axis the contribution of the smoother to the fitted values.

Contrary to the GAMM results obtained for blue sharks, no significant relationship was found between thermal fronts and foraging behaviour for mako sharks. The explained deviance R^2 obtained was -0.01 which indicates that the chosen model does not follow the trend of the data. The variance of the residuals was 0.10. The smoothing term s(logF_{comp}) was not a statistically significant variable, with an F value of 2.06 and p-value

of 0.11 (p>0.05) and an optimal number of degrees of freedom of 2.86, indicating a weak non-linear relationship between variables.

In the case of mako sharks, the smoother is centered around 0 starting a smooth decrease until a minimum of ~1.00 and increasing until it reaches a peak in ~1.75 and starts decreasing for the higher logF_{comp} values.

The GAMM analysis showed that, overall, tagged sharks preferred frontal boundary habitats with high SST gradients known to be highly productive.

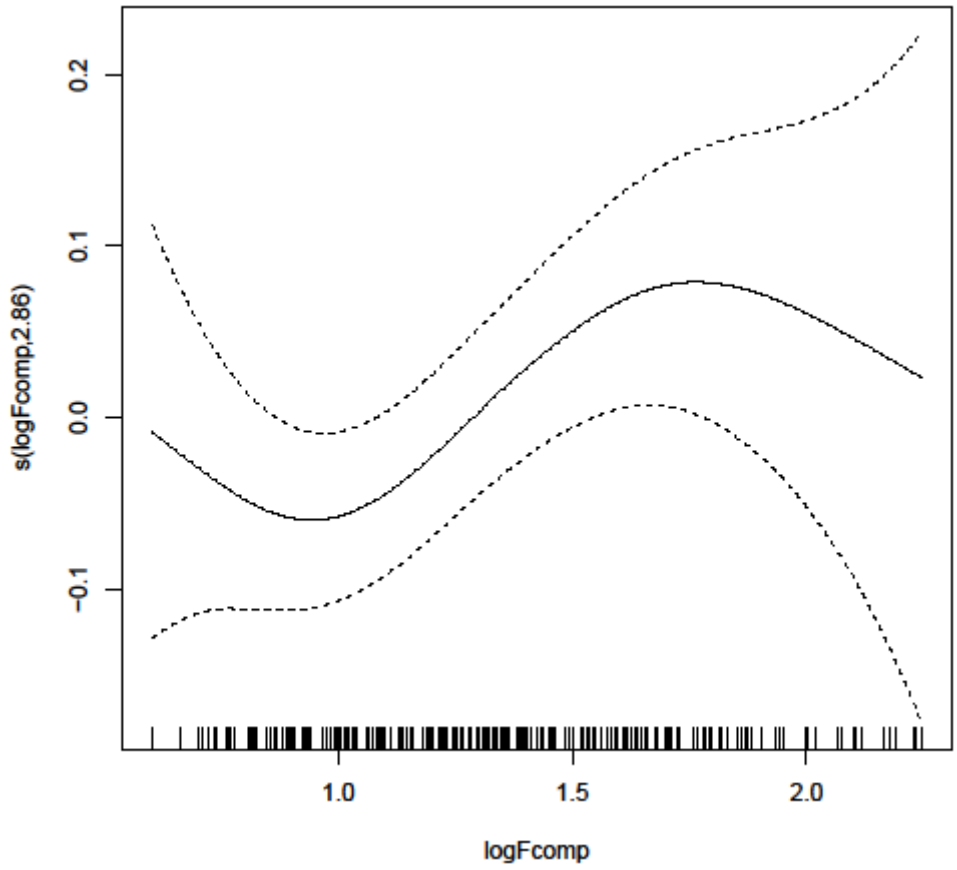


Fig. 9 - Modelling the relation between F_{comp} and FPT with a Generalized Addictive Mixed Model (GAMM) for mako sharks. GAMM revealed no significant differences in the smoothing term (p>0.001). An initial decrease in FPT is observed, starting to increase around 1.0 with the increasing F_{comp} until it reaches a pick and start a smooth decrease. Dashed lines represent 95% confidence intervals above and below the solid line representing the logFPT. The little vertical lines along the *x*-axis indicate the FPT values of individual sharks and the *y*-axis the contribution of the smoother to the fitted values.

Discussion

In this study, I used a large number of tracked sharks from two species ranging from 2006 to 2015, tagged with satellite tags in essentially three different areas of the north Atlantic Ocean. Individual sharks displayed relatively variable movement patterns across the various areas over timescales of days-weeks-months (Table 1), with one blue shark moving into the southern hemisphere (Figure 1; A14). Satellite tags provided data on the movements and space-use at different spatial scales and over longer time-periods, however, continuous advances in tracking technology brought more accurate tracking data that can be used in future investigations about habitat preference of marine vertebrates with more accurate data at finer scales, such as fast-acquisition GPS systems (Sims *et al*., 2010).

Spatial distribution

With the FPT analysis, quantification of search effort allowed the understanding of where blue and mako sharks spent more time along their pathways. The combination of FPT analysis with composite front mapping (Miller, 2009) provided a new insight into the influence of oceanic fronts in habitat selection of pelagic sharks in this study. By the observation of combined FPT data with composite front maps, there seemed to be higher FPT values in high frontal intensity areas such as the Gulf Stream and the Azores archipelago. As previously stated, higher shark densities were identified at all the locations where sharks from our study aggregated (Tittensor *et al*., 2010; Campana *et al*., 2011).

In general, blue and mako sharks had more northward movements during spring and summer and tended to spend the cold seasons in the mid-Atlantic or in more southern regions. It is also evident a site-fidelity foraging behaviour, especially in blue sharks tagged in the Azores, returning to this area during the winter. This behaviour was also identified in other shark species (Meyer *et al*., 2010; Barnett *et al*., 2011), as also in marine predators, such as seabirds (Patrick *et al*., 2014) and mammals (Foote *et al*., 2010; Irvine *et al*. 2014), and may be indicative of the knowledge about prey spatial and temporal distribution acquired from previous foraging experiences (Weimerskirch, 2007; Bost *et al*., 2009; Wakefield *et al*., 2015).

Data analysis and results

Because of the spatial and temporal auto-correlation presented in our data I opted to perform a mixed GAM analysis for modulation. It is of great importance for the model to assume that observations from different sharks are independent, likewise for tagging locations of the same shark, because without taking the inherent individual-level variability into account, tracks with more locations could bias the results. Additionally, the GAMM analysis includes a random-effect term (Pankratz, de Andrade & Therneau, 2005) which can deal with different behavioural data among individuals.

My analysis determined a high relation between the FPT and thermal fronts in blue sharks. Although several tracks were relatively short (few days), results are indicative of the association between blue sharks with these high-density prey hotspots. Previous investigations revealed associations between marine predators with coastal and oceanic fronts. For example, Scheffer *et al*. (2010) investigated the foraging strategy of king penguins (*Aptenodytes patagonicus*) in relation to both the time of the day and variation in SST in the Polar Front Zone (PFZ). They also explored how king penguins encounter predictable oceanographic mesoscale features in the PFZ to the north of South Georgia, and, consequently, how they adjust their dive and foraging behaviours. King penguins were tracked with SPOT4 and Mk 7 WildLife Computers Time Depth Recorder (TDR), between December 2005 and January 2006, at the Hound Bay colony in the north-east of South Georgia. SST data were obtained in order to investigate correlations between foraging behaviour and oceanographic conditions. The FPT analysis was calculated to determine changes in search effort of the tracked individuals. King penguins appeared to target predictable mesoscale oceanographic features in the PFZ, as the warm-core eddy and strong temperature gradients at oceanic fronts in this area. When reaching warmer waters, two different trip types could be distinguished: the direct trips, characterized by straight pathways to one foraging area, and circular trips, where birds foraged along strong thermal gradients. Giving this, different ARS patterns were identified for the two trip types. In the direct trip type, ARS was clearly concentrated in specific areas, while for the circular trip type the ARS was displayed over the whole duration of the trip. ARS patterns are correlated with the two trip types, but the direct trips seem to represent a favorable foraging strategy. There was a clear relation between the diving behaviour with water temperature and time of day, highlighting the probable influence of prey distributions in the adjustment of foraging effort and travel patterns.

In contrast, model results from mako sharks revealed no significant relation between FPT and thermal fronts. We need to take into consideration that our data from mako sharks are very small compared to that for blue sharks. I am modelling data from 44 individual blue sharks against only 4 individual mako sharks. Additionally, the tracking data from these 4 individuals is also short, ranging from 23 to 58 days, most probably representing a small portion of the track. The same problem was found in the study carried out in north-east Atlantic (Miller *et al*, 2015) where tracking data from only seven basking sharks (*Cetorhinus maximus*) were associated with seasonally persistent and contemporaneous fronts. Results indicate sharks' preference for productive regions, but obviously, these results could not be extrapolated to the population level, as it happens in the case of mako sharks from this study.

Likewise, the FPT radius had different values among species. While for blue sharks the FPT radius ranged between 25.00 and 824.70 km, for mako sharks it ranged between 58.00 and 268.55 km, which probably explains the absence of results. FPT analysis is very sensitive to telemetry error (Pinaud, 2008) and when applied at very patchy habitat conditions, it can lead to an erroneous classification of the ARS behaviour actually displayed by animals. Although I chose a common spatial scale for the studied individuals, large-scale activities may mask smaller scale behaviours (Fauchald & Tveraa 2003). Better results would be obtained if FPT radius were chosen for a finer-scale, especially in the case of sharks with short tracking data. Tracking data should be long enough so that the analysis can distinguish between extensive and sinuous movements, so probably the analysis should be re-run to identify ARS behaviour at smaller scales within the large areas of the radius with the highest variance.

In the statistic values from the GAMM, blue sharks had an R^2 value of only 0.22. Nevertheless, this low R^2 value was expected. When for example any field attempts to predict human behaviour, the R^2 values are typically lower than 50%, because humans are harder to predict than their physical processes (Frost, 2013). However, the *F*-test indicates a statistically significant relationship between variables, which means that changes in logFPT are associated with changes in logF_{comp} and thus, I can still draw important conclusions. In the case of mako sharks, the R^2 is a negative value of -0.01. It is possible to have a negative R^2 value whenever the best-fit model fits the data worse than a horizontal line.

The explanatory variable F_{comp} used in GAMM covers the frontal activity registered for the individual tracking days, giving the mean frontal activity for each of the sharks.

However, the GAMM would give more accurate results about the relation studied here when modulating monthly, weekly and daily composite front maps (F_{comp}). For example, in the case of shark M2 there is an unquestionable relation between foraging behaviour and frontal activity and probably the GAMM results for this species would give a significant relation when running with finer-scale data.

Future work

Although the interaction between oceanography and marine predators have been predominantly studied with two-dimensional data from telemetry (Wakefield *et al*., 2009) it would be of great importance to analyze vertical data, especially because blue and mako sharks are deep diving predators (Carey & Scharold, 1990; Holts & Bedford, 1993) and their behaviour may be coupled to the fine-scale horizontal and vertical distributions of their prey (Elliott *et al*., 2008; Queiroz *et al*., 2012, 2017; Boyd *et al*., 2015; Goldbogen *et al*., 2015). When studying environmental processes, composite front mapping can only detect surface frontal activity giving a two-dimensional view of a complex three-dimensional environment. Moreover, our study does not include the effects of mixed-layer depth, thermocline, chl-a fronts, oxygen concentration and other oceanographic factors found to have an influence on the habitat selection by predators (McConnell *et al*., 1992; Cotté *et al*., 2007; Nordstrom *et al*., 2013; Scales *et al*., 2014a).

In the study of Queiroz *et al*. (2017), high-resolution dive depth profiles were analyzed for blue and basking sharks, tagged with PSAT tags in the north Atlantic, to examine movement patterns in relation to environmental heterogeneity. U- and V-shaped dives were the most commonly performed by both species, representing ~70% of the total number of dives. They found that mean depth and mean depth range decreased with increasing levels of primary productivity (chl-a), whereas ascent velocities displayed a positive correlation. By combining dive profiles with horizontal movements and oceanographic gradients, blue sharks were found to forage closer to the surface in productive areas of the north Atlantic, where surface longliners also concentrate their activities (Queiroz *et al*., 2012).

In future work, horizontal interactions with frontal activity could be compared with vertical data from the same individual, incorporating other oceanographic features in these models. New improvements on tracking devices allowed collection of three-dimensional information about the behaviour of diving animals, such as altimetry of Global Positioning Systems (GPS), acoustic systems, geomagnetic intensity, dead reckoning or digital tags

(DTags), successfully used in many species of birds or marine mammals (e.g., Weimerskirch *et al*., 2002, 2005; Harcourt *et al*., 2000; Hindell *et al.,* 2002; Mitani *et al*., 2003, 2004; Davis *et al.*, 2001; Johnson & Tyack, 2003). Nevertheless, even collecting data simultaneously the analysis has always been reducing the environment to a two-dimensional space.

The proposed Spherical first-passage time (SFPT; Bailleul, Lesage & Hammill, 2010) would be able to overcome this issue. It has already been used, for example in a study at Año Nuevo State Park in the USA, where northern elephant seals (*Mirounga angustirostris*) were tracked with multisensor data loggers that recorded depth, tri-axis acceleration, tri-axis magnetism and swim speed in order to identify 3D movements and prove that underwater fine-scale movements are strongly linked to higher foraging success (Adachi *et al*., 2016). Sinuous movements of seals were quantified under the concept of volume-restricted search (VRS), analogous to ARS but in 3D, and then analyzed with SFPT on 3D dive paths coupled with data on feeding. Northern elephant seals revealed a strong link between VRA and foraging success, particularly within nested VRS zones. Such results found a hierarchical decision-making in foraging hierarchically structured prey-patches at different spatial scales.

Final Remarks and conservation contribution

Pelagic sharks' populations had declined because of the high-seas fisheries that catch thousands of these animals as by-catch (Worm *et al*., 2013). Conservation actions are urgent to prevent a catastrophic loss of these top predators. The study of Queiroz *et al*. (2016) found an extraordinary overlap between sharks' space-use and Portuguese and Spanish longline fishing vessels in the Atlantic Ocean, between 2006 and 2012. This study analyzed tracked data from blue (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), longfin mako (*Isurus paucus*), tiger (*Galeocerdo cuvier*), great hammerhead (*Sphyrna mokarran*) and scalloped hammerhead (*Sphyrna lewini*), performing 99 individuals. The analysis determined a preference for specific regions with thermal fronts and high productivity, such as the Gulf Stream and North Atlantic Current area. Also the analysis for pelagic longliner movements showed a preference for habitats with the same characteristics. Results revealed an 80% spatial overlap between longline fishing vessels and shark movements, with spatial and temporal persistence over the years. This kind of studies have such a great importance to inform the management of fisheries about the need for international catch limits of pelagic sharks.

The spatial movements of shark populations are influenced by how activity and behaviour affects rates of key movements, and by their physical and biotic environment (Sims, 2010). My analysis highlights the association between sharks and thermal fronts when searching for food (especially for blue sharks) and provide novel insights into the behavioural ecology of these two shark species.

In summary, the FPT analysis combined with composite front mapping showed to be useful in studying the foraging ecology of blue and mako sharks in the north Atlantic Ocean. Novel methodologies would improve the knowledge about distribution and habitat preferences, as the ones discussed here. Such knowledge has implications for the implementation of management and conservation solutions (Miller & Christodoulou, 2014; Scales *et al*., 2014b) and hence, contributing for the reduction of the high levels of by-catch by fisheries that has been reported for blue and mako sharks (Simpfendorfer *et al*., 2002b) with equal importance for other marine predators.

References

Aasen, O. 1963. Length and growth of the porbeagle (*Lamna nasus* Bonnaterre) in the northwest Atlantic. *Fiskeridir Skrifter Serie Havundersokelser*, 13, 20–37.

Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M., Bava, J. 2004. Marine fronts at the continental shelves of austral South America: physical and ecological processes. *Journal of Marine Systems,* 44, 83–105.

Adachi, T., Costa, D.P., Robinson, P.W., Peterson, S.H., Yamamichi, M., Naito, Y., Takahashi, A. 2016. Searching for prey in a three-dimensional environment: hierarchical movements enhance foraging success in northern elephant seals. *Functional Ecology*, 31, 361–369.

Afonso, A.S., Hazin, F.H.V. 2015. Vertical movement patterns and ontogenetic niche expansion in the tiger shark, *Galeocerdo cuvier.* PLoS ONE 10:e0116720.

Aires-da-Silva, A., Gallucci, V.F. 2007. Demographic and Risk Analysis Applied to Management and Conservation of the Blue Shark (*Prionace glauca*) in the North Atlantic Ocean. *Marine and Freshwater Research*, 58, 570–580.

Anonymous, 2009. Report of the 2008 shark stock assessment meeting. *ICCAT Collective Volume of Scientific Papers*, 64, 1343–1491.

Arendt, M.D., Boynton, J., Schwenter, J.A., Byrd, J.I., *et al*. 2012. Spatial clustering of loggerhead sea turtles in coastal waters of the NW Atlantic Ocean: implications for management surveys. *Endangered Species Research*, 18, 219−231.

Arnold, G., Dewar, H. 2001. Electronic tags in marine fisheries research. In Sibert, J.R., Nielsen, J.L. (eds) *Electronic Tagging and Tracking in Marine Fisheries*. Kluwer Academic Press, 7–64.

Bailey, H., Thompson, P. 2006. Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. *Journal of Animal Ecology*, 75, 456–465.

Bailleul, F., Lesage, V., Hammill, M.O. 2010. Spherical First Passage Time: A tool to investigate area-restricted search in three-dimensional movements. *Ecological Modelling*, 221, 1665–1673.

Barnett, A., Abrantes, K.G., Stevens, J.D., Semmens, J.M. 2011. Site fidelity and sexspecific migration in a mobile apex predator: implications for conservation and ecosystem dynamics. *Animal Behaviour*, 81, 1039–1048.

Baum, J.K., Worm, B. 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, 78, 699–714.

Benhamou, S. 1992. Efficiency of area-restricted searching behaviour in a continuous patchy environment. *Journal of Theoretical Biology*, 159, 67–81.

Block, B.A., Dewar, H., Farwell, C., Prince, E.D. 1998. A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proceedings of the National Academy of Sciences of the USA*, 95, 9384–9389.

Block, B.A., Jonsen, I.D., Jorgensen, S.J. *et al*. 2011. Tracking apex marine predator movements in a dynamic ocean. *Nature*, 475, 86–90.

Bonfil, R. 1994. Overview of world elasmobranch fisheries. *FAO Fisheries Technical Paper*, Rome, FAO, 341, 119.

Bost, C.A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C., Ainley, D.G., Weimerskirch, H. 2009. Importance of Southern Ocean fronts for seabirds and sea mammals. *Journal of Marine Systems*, 78, 363–376.

Boyd, C., Castillo, R., Hunt, G.L., Punt, A.E., VanBlaricom, G.R., Weimerskirch, H., Bertrand, S. 2015. Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey. *Journal of Animal Ecology*, 84, 1575–1588.

Boyce, D.G., Tittensor, D.P., Worm, B. 2008. Effects of temperature on global patterns of tuna and billfish richness. *Marine Ecology Progress Series*, 355, 267–276.

Bradshaw, C.J.A., Sims, D.W., Hays, G.C. 2007. Measurement error causes scale-dependent threshold erosion of biological signals in animal movement data. *Ecological Applications*, 17, 628–638.

Breed, G.A., Jonsen, I.D., Myers, R.A., Bowen, D.W., Leonard, M.L. 2009. Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by statespace analysis. *Ecology*, 90, 3209–3221.

Burger, A.E. 2003. Effects of the Juan de Fuca Eddy and upwelling on densities and distributions of seabirds off southwest Vancouver Island, British Columbia. *Marine Ornithology*, 31, 113–122.

Cailliet, G.M., Bedford, D.W. 1983. The biology of three pelagic sharks from California waters, and their emerging fisheries: a review. *California Cooperative Oceanic Fisheries Investigations Report,* 24, 57–59.

Camhi, M.D., Lauck, E., Pikitch, E.K., Babcock, E.A. 2008. *A global overview of commercial fisheries for open ocean sharks.* In Camhi, M.D., Pikitch, E.K., Babcock, E.A. (eds) *Sharks of the Open Ocean: Biology, Fisheries and Conservation.* Oxford, UK, Blackwell, 166–192.

Campana, S.E., Dorey, A., Fowler, M., Joyce, W., Wang, Z. *et al*. 2011. Migration Pathways, Behavioural Thermoregulation and Overwintering Grounds of Blue Sharks in the Northwest Atlantic. *PLoS ONE*, 6(2), e16854.

Campana, S.E., Joyce, W.N. 2004. Temperature and depth associations of porbeagle shark (*Lamna nasus*) in the northwest Atlantic. *Fisheries Oceanography*, 13, 52–64.

Campana, S.E., Joyce, W.N., Manning, M.J. 2009. Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. *Marine Ecology Progress Series*, 387, 241–253.

Carey, F.G., Scharold, J. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*, 106, 329–342.

Cayula, J.F., Cornillon, P. 1992. Edge Detection Algorithm for SST Images. *Journal of Atmospheric and Oceanic Technology,* 9, 67–80.

Clarke, M.R., Clarke, D.C., Martins, H.R., Da Silva, H.M. 1996. The diet of the blue shark (*Prionace glauca* L.) in Azorean waters. *Arquipelago – Life Marine Sciences*, 14, 41–56.

Chambault, P., Pinaud, D., Vantrepotte, V., Kelle, L., Entraygues, M., Guinet, C. *et al*. 2015. Dispersal and Diving Adjustments of the Green Turtle Chelonia mydas in Response to Dynamic Environmental Conditions during Post-Nesting Migration. *PLoS ONE*, 10(9), e0137340.

Collette, B.B., Klein-MacPhee, G. (eds) 2002. *Bigelow and Schroeder's Fishes of the Gulf of Maine*, 3rd ed., Washington, DC, Smithsonian Institution Press, 748.

Compagno, L.J.V. 1984. FAO Species Catalogue. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1 – Hexanchiformes to Lamniformes. Rome, *FAO Fisheries Synopsis*, No. 125, 4, 295.

Compagno, L.J.V. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). Rome, *FAO Species Catalogue for Fishery Purposes*, No. 1, 2, 269.

Compagno, L.J.V., Fowler, S.L., Dando, M. 2005. A field guide to the sharks of the world. *Princeton University Press*, 496.

Cortés, E. 2000. Life history patterns and correlations in sharks. *Reviews in Fisheries Science*, 8, 299–344.

Costa, D.P., Burns, J.M., Crocker, D.E., Fedak, M.A., Trumble, S., Gales, N. 2001. Winter foraging ecology of crabeater seals. *American Zoology,* 41, 1417.

Cotté, C., Park, Y.H., Guinet, C., Bost, C.A. 2007. Movements of foraging king penguins through marine mesoscale eddies. *Proceedings of the Royal Society B*, 274, 2385–2391.

Davis, R.W., Fuiman, L.A., Williams, T.M., Le Boeuf, B.J. 2001. Three-dimensional movements and swimming activity of a northern elephant seal. *Comparative Biochemistry and Physiology Part: A,* 131, 759–770.

De Metrio, G., Arnold, G.P., De la Serna, J.M., Megalofonou, P., Sylos Labini, G., Deflorio, M., Buckley, A. *et al*. 2005. *Movements and migrations of North Atlantic bluefin tuna tagged with pop-up satellite tags*. In Spedicato, M.T., Lembo, G., Marmulla, G. (eds) *Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe.* Ustica, Italy, 9-13 June 2003. Rome, FAO/COISPA, 295.

De Monte, S., Cotté, C., d'Ovidio, F., Lévy, M., Le Corre, M., Weimerskirch, H. 2012. Frigatebird behaviour at the ocean–atmosphere interface: integrating animal behaviour with multi-satellite data. *Journal of the Royal Society Interface*, 9, 3351–3358.

Dent, F., Clarke, S. 2015. *State of the global market for shark products*. Rome, *FAO Fisheries and Aquaculture Technical Paper*, No 590, 190.

Domeier, M.L., Nasby-Lucas, N. 2008. Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Marine Ecology Progress Series*, 370, 221–237.

Dragon, A.C., Bar-Hen, A., Monestiez, P., Guinet, C. 2012. Comparative analysis of methods for inferring successful foraging areas from Argos and GPS tracking data. *Marine Ecology Progress Series*, 452, 253–267.

Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.V.J., Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martínez, J., Musick, J.A., Soldo, A., Stevens, J.D., Valenti, S. 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks. *Aquatic Conservation*, 18, 459–482.

Eckert, S.A., Dolar, L.L., Kooyman, G.L., Perrin, W., Rahman, R.A. 2002. Movements of whale sharks (*Rhincodon typus*) in south-east Asian waters as determined by satellite telemetry. *Journal of Zoology*, 257, 111–115.

Eckert, S.A., Stewart, B.S. 2001. Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean. *Environmental Biology of Fishes*, 60, 299–308.

Elliott, K.H., Davoren, G.K., Gaston, A.J. 2008. Time allocation by a deep-diving bird reflects prey type and energy gain. *Animal Behaviour*, 75, 1301–1310.

Etnoyer, P., Canny, D., Mate, B., Morgan, L. 2004. Persistent pelagic habitats in the Baja California to Bering Sea (B2B) ecoregion. *Oceanography*, 17, 90–101.

Farnsworth, K.D., Beecham, J.A. 1999. How do grazers achieve their distribution? A continuum of models from random diffusion to the ideal free distribution using biased random walks. *American Naturalist*, 153, 509– 526.

Fauchald, P. 1999. Foraging in a hierarchical patch system. *American Naturalist,* 153, 603–613.

Fauchald, P., Tveraa, T. 2003. Using first passage time in the analysis of area restricted search and habitat selection. *Ecology*, 84, 282–288.

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K. 2010. Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, 13, 1055–1071.

Field, I., Hindell, M., Slip, D., Michael, K. 2001. Foraging strategies of southern elephant seals (*Mirounga leonina*) in relation to frontal zones and water masses. *Antarctic Science*, 13, 371–379.

Fiedler, P.C., Bernard, H.J. 1987. Tuna aggregation and feeding near fronts observed in satellite imagery. *Continental Shelf Research*, 7, 871–881.

Foote, A.D., Simila, T., Vikingsson, G.A., Stevick, P.T. 2010. Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evolutionary Ecology*, 24, 803–814.

Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308, 1621–1623.

Franks, P.J.S. 1992. Phytoplankton blooms at fronts: patterns, scales, and physical forcing mechanisms. *Reviews in Aquatic Science*, 6, 121–137.

Frisk, M.G., Miller, T.J., Fogarty, M.J. 2001. Estimation and Analysis of Biological Parameters in Elasmobranch Fishes: a Comparative Life History Study. *Canadian Journal of Fisheries and Aquatic Sciences,* 58, 969–981.

Frost, J. 2013. Regression Analysis: How Do I Interpret R-squared and Asses the Goodness-of-Fit? [Online] Available: http://blog.minitab.com/blog/adventures-in-statistics-2/regression-analysis-how-do-i-interpret-r-squared-and-assess-the-goodness-of-fit, [Accessed 27 September 2017].

Gelfand, A., Banerjee, S., Gamerman, D. 2005. Spatial process modelling for univariate and multivariate dynamic spatial data. *Environmetrics*, 16, 465–479.

Goldbogen, J.A., Hazen, E.L., Friedlaender, A.S., Calambokidis, J., DeRuiter, S.L., Stimpert, A.K., Southall, B.L. 2015. Prey density and distribution drive the three-dimensional foraging strategies of the largest filter feeder. *Functional Ecology*, 29, 951–961.

Grémillet, D. *et al*. 2008. Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions. *Journal of Applied Ecology*, 45, 610–621.

Guinet, C., Koudil, M., Bost, C.A., Durbec, J.P., Georges, J.Y., Mouchot, M.C., Jouventin, P. 1997. Foraging behaviour of satellite-tracked king penguins in relation to sea-surface temperatures obtained by satellite telemetry at Crozet Archipelago, a study during three austral summers. *Marine Ecology Progress Series*, 150, 11–20.

Hamer, K., Humphreys, E., Magalhaes, M., Garthe, S. *et al*. 2009. Fine scale foraging behaviour of a medium ranging marine predator. *Journal of Animal Ecology,* 78, 880−889.

Hanan, D.A., Holts, D.B., Coan, A.L. Jr. 1993. The California drift gill net fishery for sharks and swordfish, 1981–82 through 1990–91. *Fishery Bulletin,* (Washington DC), 175, 89–95.

Harcourt, R.G., Hindell, M.A., Bell, D.G., Waas, J.R. 2000. Three-dimensional dive profiles of free-ranging Weddell seals. *Polar Biology*, 23, 479–487.

Hastie, T.J., Tibshirani, R.J. 1990. *Generalized additive models.* Chapman and Hall, London, xv–335.

Hays, G., Hobson, V.L., Metcalfe, J.D., Righton, D., Sims, D.W. 2006. Flexible foraging movements of leatherback turtles across the North Atlantic. *Ecology*, 87, 2647–2656.

Heithaus, M.R., Dill, L.M., Marshall, G.J., Buhleier, B. 2002. Habitat use and foraging behaviour of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology,* 140, 237–248.

Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution,* 23, 202–210.

Henderson, A.C., Dunne, J., Flannery, K. 2001. Observations on the biology and ecology of the blue shark in the North-East Atlantic. *Journal of Fish Biology*, 58, 1347–1358.

Hindell, M.A., Harcourt, R., Waas, J.R., Thompson, D. 2002. Fine-scale threedimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii*. *Marine Ecology Progress Series,* 242, 275–284.

Holts, D.B., Bedford, D.W. 1993. Horizontal and vertical movements of the shortfin mako, *Isurus oxyrinchus*, in the Southern California Bight. *Australian Journal of Marine Freshwater Research,* 44, 45–60.

Holts, D.B., Julian, A., Sosa-Nishizaki, O., Bartoo, N.W. 1998. Pelagic shark fisheries along the west coast of the United States and Baja California, Mexico. Fisheries *Research*, 39, 115–125.

Hoolihan, J.P., Luo, J. 2007. Determining summer residence status and vertical habitat use of sailfish (*Istiophorus platypterus*) in the Arabian Gulf. *ICES Journal of Marine Science*, 64, 1791–1799.

Irvine, L.M., Mate, B.R., Winsor, M.H., Palacios, D.M., Bograd, S.J., Costa, D.P. *et al*. 2014. Spatial and temporal occurrence of blue whales off the US West Coast, with implications for management. *PLoS ONE,* 9, e102959.

Johnson, A.R., Wiens, J.A., Milne, B.T., Crist, T.O. 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology*, 7, 63–75.

Johnson, C.J., Parker, K.L., Heard, D.C., Gillingham, M.P. 2002. Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology*, 71, 225–235.

Johnson, M., Tyack, P.L. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *Journal of Ocean Engineering,* 28, 3–12.

Largier, J.L. 1993. Estuarine fronts: how important are they? *Estuaries*, 16, 1–11.

Lutcavage, M.E., Brill, R.W., Skomal, G.B., Chase, B.C., Howey, P.W. 1999. Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 173–177.

Kessel, S.T., Chapman, D.D., Franks, B.R., Gedamke, T. *et al*. 2014. Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris)*. *Marine Ecology Progress Series*, 514, 175−190.

Kohler, N.E., Turner, P.A. 2008. Stock *structure of the blue shark (Prionace glauca) in the North Atlantic Ocean based on tagging data.* In Camhi, M., Pikitch, E., Babcock, E. (eds) *Sharks of the Open Ocean: Biology, Fisheries and Conservation.* Oxford, UK, Blackwell Publishing, 339–348.

Lowe, C.G., Bray, R.N. 2006. *Fish movement and activity patterns*. In Allen, L., Pondella, D.P., Horn, M. (eds) *The Ecology of Marine Fishes: California and Adjacent Waters*. Berkeley, University of California Press, 524-553.

Mandelman, J.W., Cooper, P.W., Werner, T.B., Lageux, K.M. 2008. Shark bycatch and depredation in the U.S. Atlantic pelagic longline fishery. *Reviews in Fish Biology and Fisheries*, 18, 427–442.

Mann, K.H., Lazier, J.R.N. 1991. Dynamics of marine ecosystems, biological-physical interactions in the oceans. *Blackwell Scientific Publications*, Boston, 49, 272–273.

Mate, B.R., Krutzikowsky, G.K., Winsor, M.H. 2000. Satellite-monitored movements of radio-tagged bowhead whales in the Beaufort and Chukchi seas during the late-summer feeding season and fall migration. *Canadian Journal of Zoology*, 78, 1168–1181.

McConnell, B., Chambers, C., Fedak, M. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science*, 4, 393–398.

Mearns, A.J., Young, D.R., Olson, R.J., Schafer, H.A. 1981. Trophic structure and the cesium-potassium ratio in pelagic food webs. *California Cooperative Oceanic Fisheries Investigations Report*, 22, 99–110.

Mejuto, J., Garcia-Cortés, B., Ramos-Cartelle, A., de la Serna, J.M. 2008. Scientific estimations of bycatch landed by the Spanish surface longline fleet targeting swordfish (*Xiphias gladius*) in the Atlantic Ocean with special reference to the years 2005 and 2006. *ICCAT Standing Committee on Research and Statistics*, Doc 2008/045.

Metcalfe, J.D., Arnold, G.P. 1997. Tracking fish with electronic tags. *Nature*, 387, 665–666.

Meyer, C.G., Papastamatiou, Y.P., Holland, K.N. 2010. A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. *Marine Biology*, 157, 1857–1868.

Miller, P.I. 2009. Composite front maps for improved visibility of dynamic sea-surface features on cloudy SeaWiFS and AVHRR data. *Journal of Marine Systems*, 78, 327-336.

Miller, P.I. 2016. Detection and Visualization of Oceanic Fronts from Satellite Data, with Applications for Fisheries, Marine Megafauna and Marine Protected Areas. *International Journal of Remote Sensing*, 25, 1437–1442.

Miller, P.I., Christodoulou, S. 2014. Frequent locations of oceanic fronts as an indicator of pelagic diversity: application to marine protected areas and renewables. *Marine Policy,* 45, 318–329.

Miller, P.I., Scales, K.L., Ingram, S.N., Southall, E.J., Sims, D.W. 2015. Basking sharks and oceanographic fronts: quantifying associations in the north-east Atlantic. *Functional Ecology*, 29, 1099–109.

Mitani, Y., Sato, K., Ito, S., Cameron, M.F., Siniff, D.B., Naito, Y. 2003. A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: results from two lactating Weddell seals. *Polar Biology,* 26, 311–317.

Mitani, Y., Watanabe, Y., Sato, K., Cameron, M.F., Naito, Y. 2004. 3D diving behaviour of Weddell seals with respect to prey accessibility and abundance. *Marine Ecology Progress Series,* 281, 275–281.

Mitchell, J.D., Collins, K.J., Miller, P.I., Suberg, L.A. 2014. Quantifying the impact of environmental variables upon catch per unit effort of the blue shark *Prionace glauca* in the western English Channel*. Journal of Fish Biology*, 85, 657−670.

Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., Peterson, C.H. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean*. Science*, 315, 1846–1850.

Myers, R.A., Worm, B. 2005. Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360, 13–20.

Nams, V.O. 2005. Using animal movement paths to measure response to spatial scale. *Oecologia*, 143, 179–188.

Nathan, R. 2008. An emerging movement ecology paradigm. *Proceeding of the National Academy of Sciences USA*, 105, 19050–19051.

Nakano, H., Nagasawa, K. 1996. Distribution of pelagic elasmobranches caught by salmon research gillnets in the North Pacific. *Fisheries Science,* 62, 860–865.

Nakano, H., Stevens, J.D. 2008. *The biology and ecology of the blue shark, Prionace glauca. Sharks of the open ocean: biology, fisheries and conservation*. In Camhi, M.D., Pikitch, E.K., Babcock, E.A. (eds) Oxford, UK, Blackwell Scientific Publications, 140–151.

Neilson, J.D., Smith, S., Roter, F., Paul, S.D., Porter, J.M., Lutcavage, M. 2009. *Investigations of horizontal movements of Atlantic swordfish using pop-up satellite archival tags.* In Nielsen, J.L., Arrizabalaga, H., Fragoso, N., Hobday, A., Lutcavage, M., Sibert, J. *Tagging and Tracking of Marine Animals with Electronic Devices*. London, Springer, 145–159.

Nichols, W.J., Resendiz, A., Seminoff, J.A., Resendiz, B. 2000. Transpacific migration of a loggerhead turtle monitored by satellite telemetry*. Bulletin of Marine Science*, 67, 937–947.

Nordstrom, C.A., Battaile, B.C., Cotté, C., Trites, A.W. 2013. Foraging habtats of lactating northern fur seals are structured by thermocline depths and submesoscale fronts in the eastern bering sea. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 88–89, 78–96.

Oschlies, A., Garçon, V. 1998. Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. *Nature*, 394, 266–269.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, 14, 483–488.

Pade, N.G. *et al*. 2009. First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: area fidelity, wider-scale movements and plasticity in diel depth changes. *Journal of Experimental Marine Biology and Ecology*, 370, 64-74.

Pankratz, V.S., de Andrade, M., Therneau, T.M. 2005. Random-effects Cox proportional hazards model: general variance components methods for time-to-event data. *Genetic Epidemiology,* 28, 97–109.

Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O., Matthiopoulos, J. 2008. State-space models of individual animal movement. *Trends in Ecology and Evolution*, 23, 87–94.

Pinaud, D. 2008. Quantifying search effort of moving animals at several spatial scales using first-passage time analysis: effect of the structure of the environment and tracking systems. *Journal of Applied Ecology*, 45, 91–99.

Pinaud, D., Weimerskirch, H. 2005. Scale-dependent habitat use in a long-ranging central place predator. *Journal of Animal Ecology*, 74, 852–863.

PFMC. 2003. Pacific Fishery Management Council Fishery Management Plan and Environmental Impact Statement for US West Coast Fisheries for Highly Migratory Species. Portland, OR.

Podesta, G.P., Browder, J.A., Hoey, J.J. 1993. Exploring the association between swordfish catch rates and thermal fronts on United-States longline grounds in the Western North-Atlantic*. Continental Shelf Research*, 13, 253–277.

Priede, I.G., Miller, P.I. 2009. A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing II: New analysis reveals orientation to a thermal front. *Fisheries Research*, 95, 370–372.

Prince, E.D., Goodyear, C.P. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fisheries Oceanography*, 15, 451–464.

Queiroz, N., Humphries, N.E., Mucientes, G., Hammerschlag, N., Lima, F.P., Scales, K.L., Miller, P.I., Sousa, L.L., Seabra, R., Sims, D.W. 2016. Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *Proceeding of the National Academy of Sciences*, 113, 1582-1587.

Queiroz, N., Humphries, N.E., Noble, L.R., Santos, A.M., Sims, D.W. 2012. Spatial Dynamics and Expanded Vertical Niche of Blue Sharks in Oceanographic Fronts Reveal Habitat Targets for Conservation. Ropert-Coudert, Y. (ed). *PLoS ONE*, 7:e32374.

Queiroz, N., Vila-Pouca, C., Couto, A., Southall, E.J., Mucientes, G., Humphries, N.E. Sims, D.W. (2017) Convergent Foraging Tactics of Marine Predators with Different Feeding Strategies across Heterogeneous Ocean Environments. *Frontiers in Marine Science,* 4, 239.

Ramírez-Macías *et al*. 2017. Oceanic adults, coastal juveniles: tracking the habitat use of whale sharks off the Pacific coast of Mexico*. PeerJ*, 5:e3271.

R Core Team 2016. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. [Online] Available: www.R-project.org.

Rogers, P.J., Huveneers, C., Page, B., Goldsworthy, S.D. *et al*. 2015. Living on the continental shelf edge: habitat use of juvenile shortfin makos *Isurus oxyrinchus* in the Great Australian Bight, southern Australia. *Fisheries Oceanography*, 24, 205−218.

Royer, F., Fromentin, J.M., Gaspar, P. 2004. Association between bluefin tuna schools and oceanic features in the western Mediterranean. *Marine Ecology Progress Series*, 269, 249–263.

Scales, K.L., Miller, P.I., Embling, C.B., Ingram, S.N., Pirotta, E., Votier, S.C. 2014a. Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *Journal of the Royal Society Interface*, 11, 20140679.

Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W., Votier, S.C. 2014b. On the front line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, 51, 1575–1583.

Scales, K.L., Miller, P.I., Varo-Cruz, N., Hodgson, D.J., Hawkes, L.A., Godley, B.J. 2015. Oceanic loggerhead turtles *Caretta caretta* associate with thermal fronts: evidence from the Canary Current Large Marine Ecosystem. *Marine Ecology Progress Series*, 519, 195–207.

Shepherd, T.D., Myers, R.A. 2005. Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecology Letters*, 8, 1095–1104.

Scheffer, A., Trathan, P.N., Collins, M. 2010. Foraging behaviour of King Penguins (*Aptenodytes patagonicus*) in relation to predictable mesoscale oceanographic features in the Polar Front Zone to the north of South Georgia. *Progress in Oceanography*, 86, 232–245.

Simpfendorfer, C.A., Hueter, R.E., Bergman, U., Connett, S.M.H. 2002b. Results of a fishery-independent survey for pelagic sharks in the western Atlantic, 1977–1994. *Fisheries Research,* 55, 175–192.

Sims, D.W. 2010. *Tracking and analysis techniques for understanding free-ranging shark movements and behaviour. Biology of Sharks and their Relatives.* In Carrier, J., Heithaus, M., Musick, J. (eds) *Sharks and their Relatives II: Biodiversity, Adaptive physiology and conservation.* Boca Raton, Florida, CRC Press, 2, 351–392.

Sims, D.W., Quayle, V.A. 1998. Selective foraging behaviour of basking sharks on zooplankton in a smallscale front. *Nature,* 393, 460–464.

Stainiland, I.J., Robinson, S.L. 2008. Segregation between the sexes: Antarctic fur seals, *Arctocephalus gazella*, foraging at South Georgia. *Animal Behaviour*, 75, 504–512.

Stevens, J.D. 1990. Further results from a tagging study of pelagic sharks in the north-east Atlantic. *Journal of Marine Biology Association of the United Kingdom,* 70, 707–720.

Stevens, J.D., Bonfil, R., Duvly, N.K., Walker, P.A. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystem. *ICES Journal of Marine Science*, 57, 476–494.

Stillwell, C.E., Kohler, N.E. 1982. Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 407– 414.

Stokesbury, M.J.W., Cosgrove, R., Boustany, A.M., Browne, D., Teo, S.L.H., O'Dor, R.K., Block, B.A. 2007. Results of satellite tagging of Atlantic bluefin tuna, *Thunnus thynnus*, off the coast of Ireland. *Hydrobiologia,* 58, 91–97.

Strickland, C., Simpson, D., Turner, I., Denham, R., Mengersen, K. 2011. Fast Bayesian analysis of spatial dynamic factor models for multitemporal remotely sensed imagery models for spatiotemporal data. *Journal of the Royal Statistical Society C - Applied Statistics*, 60, 109–124.

Stroud, J., Muller, P., Sanso, B. 2001. Dynamic models for spatiotemporal data. *Journal of the Royal Statistical Society B*, 63, 673–689.

Suryan, R.M., Sato, F., Balogh, G.R. *et al*. 2006. Foraging destinations and marine habitat use of short-tailed albatrosses: a multi-scale approach using first-passage time analysis. *Deep-Sea Research*, 2, 370–386.

Taillade, M. 1992. *Animal tracking by satellite*. In Priede, I.G., Swift, S.M. (eds) *Wildlife telemetry: remote monitoring and tracking of animals.* London, Ellis Horwood, 149–160.

Thums, M., Bradshaw, C.J.A., Hindell, M.A. 2011. In situ measures of foraging success and prey encounter reveal marine habitat-dependent search strategies. *Ecology*, 92, 1258–1270.

Tittensor, D.P. *et al*. 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature*, 466, 1098–1101.

Tremblay, Y., Roberts, A.J., Costa, D.P. 2007. Fractal landscape method: an alternative approach to measuring area-restricted searching behaviour. *Journal of Experimental Biology*, 210, 935–945.

Ullman, D.S., Cornillon, P.C. 1999. Satellite-derived sea surface temperature fronts on the continental shelf off the northeast US coast. *Journal of Geophysical Research-Oceans*, 104, 23459–23478.

Vandeperre, F., Aires-da-Silva, A., Fontes, J., Santos, M., Serrão Santos, R., Afonso, P. 2014. Movements of Blue Sharks (*Prionace glauca*) across Their Life History. *PLoS ONE*, 9(8), e103538.

Vaudo, J.J., Wetherbee, B.M., Wood, A.D., Weng, K., Howey-Jordan, L.A., Harvey, G.M., Shivji, M.S. 2016. Vertical movements of shortfin mako sharks *Isurus oxyrinchus* in the western North Atlantic Ocean are strongly influenced by temperature*. Marine Ecology Progress Series,* 547, 163–175.

Vlietstra, L.S., Coyle, K.O., Kachel, N.B., Hunt, G.L. 2005. Tidal front affects the size of prey used by a top marine predator, the short-tailed shearwater (*Puffinus tenuirostris*). *Fisheries Oceanography*, 14, 196–211.

Voegeli, F.A., Smale, M.J., Webber, D.M., Andrade, Y., O' Dor, R.K. 2001. Ultrasonic telemetry, tracking and automated monitoring technology for sharks. Environmental Biology of Fishes, 60, 267–281.

Wall, S.M., Bradshaw, C.J.A., Southwell, C.J., Gales, N.J., Hindell, M.A. 2007. Crabeater seal diving behaviour in eastern Antarctica. *Marine Ecology Progress Series*, 337, 265–277.

Walsh, P.D. 1996. Area-restricted search and the scale dependence of patch quality discrimination. *Journal of Theoretical Biology,* 183, 351–361.

Wakefield, E.D. *et al*. 2015. Long-term individual foraging site fidelity—why some gannets don't change their spots*. Ecology*, 96, 3058–3074.

Wakefield, E.D., Phillips, R.A., Matthiopoulos, J. 2009. Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series*, 391, 165–182.

Wildlife Computers. 2016. SPOT. [Online] Available: http://wildlifecomputers.com/our-tags/spot/, [Accessed: 14 December 2016].

Wilson, R.P., Ducamp, J.J., Rees, W.G., Culik, B.M., Niekamp, K. 1992. *Estimation of location: global coverage using light intensity*. In Priede, I.G., Swift, S.M. (eds) *Wildlife*

telemetry: remote monitoring and tracking of animals. Chichester, UK, Ellis Horwood, 131–134.

Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabille, G., Dell'Omo, G., Lipp, H.P. 2002. GPS tracking of foraging albatrosses*. Science*, 295, 1259.

Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A., Marsac, F. 2005. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? *Proceedings of the Royal Society B*, 272, 53–61.

Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? *Deep-Sea Research Part II Topical Studies in Oceanography*, 54, 211–223.

Weng, K.C., Castilho, P.C., Morrissette, J.M., Landeira-Fernandez, A.M., Holts, D.B. *et al*. 2005. Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science*, 310, 104–106.

Weng, K.C., Foley, D.G., Ganong, J.E., Perle, C., Shillinger, G.L., Block, B.A. 2008. Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Marine Ecology Progress Series*, 372, 253–264.

Wood, S.N. 2006. Generalized Additive Models: An Introduction with R. *Chapman and Hall/CRC Texts in Statistical Science,* 16, 410.

Worm, B., Lotze, H.K., Myers, R.A. 2003. Predator diversity hotspots in the blue ocean. *Proceeding of the National Academy of Sciences,* 100, 9884–9888.

Worm, B., Sandow, M., Oschlies, A., Lotze, H.K., Myers, R.A. 2005. Global patterns of predator diversity in the open oceans. *Science*, 309, 1365–1369.

Worm, B. *et al*. 2013. Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy,* 40, 194–204.

Yoder, J.A., Ackleson, S.G., Barber, R.T., Flament, P., Balch, W.M. 1994. A line in the sea. *Nature,* 371, 689–692.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M. 2009. Mixed effects modes and extensions in ecology with R, Chapter 12, Generalized estimating equations. New York, Springer, 1, 295–321.

Annexes

Annex I

Table 2 – Radii values (m) with the corresponding maximum variance for individual sharks obtained after running the FPT analysis.

Shark ID	Name	Radii	Variance
40392	M1	268548.00	0.04
40393	M2	119975.00	0.45
135933	M3	58242.60	0.34
135934	M4	100016.00	0.22
40390	S1	37409.70	0.06
66951	S2	37409.73	0.06
66952	S3	57458.66	0.10
66954	S4	74719.41	0.10
66955	S5	27552.73	0.03
66957	S6	446025.51	0.07
66963	S7	25000.00	0.02
66967	S8	34504.18	0.20
66969	S9	41077.25	0.61
66970	S10	29946.67	0.08
84174	S11	36441.43	0.06
84175	S12	79287.39	0.16
132044	S13	39500.56	0.66
133669	S14	604637.00	0.67
133670	S15	381558.70	0.34
135925	S16	68376.43	0.17
135926	S17	201083.57	0.25
135927	S18	36822.09	0.03
135928	S19	25000.00	0.17
135929	S20	63702.44	0.04
135930	S21	25000.00	0.06
135931	S22	51863.84	0.06
135932	S23	85636.19	0.36
1	A1	60499.73	0.50
2	A2	274269.48	0.46

3	A3	96835.07	0.08
4	A4	25000.00	0.29
5	A5	29772.50	0.18
6	A6	395462.81	0.23
12	A7	32928.23	1.31
13	A8	121263.59	0.88
14	A9	633519.25	0.26
10	A10	62723.04	0.16
15	A11	36266.78	0.32
18	A12	105755.11	0.61
22	A13	54852.39	1.28
25	A14	824698.38	0.38
26	A15	152951.65	1.60
28	A16	131190.57	0.35
30	A17	116483.11	0.30
31	A18	37324.73	2.49
33	A19	169982.70	0.18
34	A20	48627.93	2.01
35	A21	134095.36	1.44